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BIOLOGY OF
SUBMERGED AQUATIC MACROPHYTE COMMUNITIES
IN THE LOWER CHESAPEAKE BAY

Volume III

Interactions of Resident Consumers in a Temperate Estuarine Seagrass Community: Vaucluse Shores, Virginia, USA.

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16. ABSTRACT

As a part of the Functional Ecology Program on Chesapeake Bay submerged aquatic vegetation (SAV), this study investigated infaunal and epifaunal trophic dynamics. The work was conducted in conjunction with other major aspects of the program (see Volumes I, II, IV) and respresnts the culmination of four years of intensive field and laboratory investigations.

The main study area established for investigating the functional ecology of resident consumers in the lower Chesapeake Bay was a large grass bed located at Vaucluse Shores on the bayside of Virginia's eastern shore. Vaucluse Shores was chosen as the study site because: (1) the site had been previously studied and background information was available; (2) the bed is well established and historically stable; (3) the area is relatively remote and unperturbed; (4) the bed contained the two dominant lower Bay macrophyte species, *Zostera marina* and *Ruppia maritima*; and (5) the bed was large enough to simultaneously accommodate varied studies and sampling regimes. This bed was intensively mapped in 1978 and 1979, and permanent transects were established for sampling reference points.

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Finally, a hearty thank you to those whose contributions we may have overlooked.

PREFACE

One of the most notable features about habitats with submerged aquatic vegetation (SAV) is the characteristically high density of the associated fauna. Included are epibiota and infauna which are represented by a diverse and complex assemblage of micro- and macroalgae, protozoans, hydrozoans, anthozoans, turbellarians, gastropods, isopods, amphipods, polychaetes, oligochaetes, bivalves, decapods and barnacles. Many of these groups exhibit distinct seasonal pulses of abundance depending on their individual spawning periods. The epibiotic community within grass beds is quite distinct from the communities in adjacent unvegetated areas. Due to the lack of a suitable substrate, there is usually very little epifauna in bare sand or mud areas. The epibiota primarily use the blades as a substratum for attachment (i.e. barnacles, algae, hydroids, etc.) or feeding platform in the case of micro herbivores grazing on the microalgae that colonize the blades. Thus, grass beds provide substrates, protection and food resources which allow for the maintenance of high densities which in turn attract and trophically support numerous migratory utilizers of SAV habitats, i.e. crabs, fishes and waterfowl. These features are fundamental to the resource value of SAV beds on a world wide basis.

The fact that numerous species of epibiota associated with SAV may not be totally dependent for their survival on the presence of grass (since many can exist on almost any biotic or abiotic substrate) does not detract from the importance of SAV. Submerged vegetation is a renewable resource, unlike many other substrates, and so persists through time.

The infaunal community also appears to benefit from the presence of SAV. This community is quite distinct from that of adjacent unvegetated areas. There is a tremendous increase in the numbers of species and individuals in vegetated habitats which is in part related to increased sediment stability, microhabitat complexity, greater food supply and decreased predation pressure. The motile community consisting of larger macroinvertebrate species (e.g. shrimp, crabs, and fish) is also diverse and distinct from surrounding unvegetated areas.

Migratory waterfowl species such as Canada geese, redheads and widgeon are closely associated with beds of submerged grasses because of the importance of the grass as a food resource. Abundances of certain waterfowl species which depend on submerged grasses for food have declined in the Chesapeake Bay in conjunction with the decline of Bay grasses during the last 15-20 years.

The trophic function of SAV communities and the refuge factor that SAV provides appear to be the key to understanding the role these habitats play in supporting living resources of direct importance to man. These two attributes are so functionally interrelated that, although it may be necessary to separate the two for the purpose of modelling the system, they must be addressed with a unified research approach.

Our study on the functional ecology of resident consumers as a part of the Functional Ecology Program on Chesapeake Bay SAV was concerned with an investigation of infaunal and epifaunal trophic dynamics. This work was conducted in conjunction with the other major aspects of the program (see Volumes I, II, IV) and represents the culmination of four years of intensive field and laboratory investigations involving many dedicated co-workers.

The main study area established for investigating the functional ecology of resident consumers in the lower Chesapeake Bay was a large grass bed located at Vaucluse Shores on the bayside of Virginia's eastern shore. Vaucluse Shores was chosen as the study site because: 1) The site had been previously studied and background information was available; 2) the bed is well established and historically stable; 3) the area is relatively remote and unperturbed; 4) the bed contained the two dominant lower Bay macrophyte species, Zostera marina and Ruppia maritima; and 5) the bed was large enough to simultaneously accomodate varied studies and sampling regimes. This bed was intensively mapped in 1978 and 1979, and permanent transects were established for sampling reference points.

Our initial effort in examining the functional ecology of resident consumers was to determine the structural aspects of the grassbed community compared to unvegetated areas (Chapter 1). We subsequently conducted predator exclusion experiments to determine the role of predation in structuring the biotic community in grassbeds (Chapter 2) and examined in greater detail predator-prey interactions in vegetated habitats (Chapter 3). Having established which species were numerically dominant, we calculated the secondary production of those species which were trophically or functionally important (Chapter 4). We then focused our attention on one dominant species, an herbivorous grazer, and examined its role in controlling epiphytic fouling on Zostera marina (Chapter 5). Because waterfowl have been the least studied trophic components of the grass bed systems in the lower Bay, we determined the intensity of utilization by wintering waterfowl of the Vaucluse grass system (Chapter 6). We also measured the impact of feeding by one species (Buffleheads) on the density of macroinvertebrate population densities. Finally, we tried to place into perspective major trophic links in the Vaucluse Shores grassbed by examining natural carbon isotope ratios (^{13}C to ^{12}C) in some of the dominant species (Chapter 7). Such an approach enabled us to determine the sources of primary production utilized by the resident consumers.

We have written each chapter as a unit to allow for easier presentation of the data and to facilitate the submission of discrete sections to peer reviewed scientific journals. Chapter 5 has already been accepted for publication in Aquatic Botany and other chapters are being redrafted for publication at a later date. Although some chapters lack comprehensive statistical analyses and data interpretation, our goals are to thoroughly conduct such revisions prior to publishing our findings. These products will be available in journals at a future date.

CHAPTER 1

STRUCTURAL ANALYSIS OF BENTHIC COMMUNITIES ASSOCIATED WITH VEGETATED AND UNVEGETATED HABITATS

by

Jacques van Montfrans

and

Robert J. Orth

ABSTRACT

Three distinct habitats in the lower eastern Chesapeake Bay (Vaucluse Shores at the mouth of Hungars Creek) were compared based on a structural analysis of the associated fauna. These habitats included a grassbed (*Zostera marina* and *Ruppia maritima*), large sand patches within the grassbed, and an offshore sand bar system. Within the vegetated habitat, comparisons were made of the fauna associated with pure stands of *Z. marina*, pure stands of *R. maritima* and mixed stands of both species.

Generally there was a trend towards a greater species diversity (Shannon H') and abundance of infaunal species and individuals in the vegetated habitats than in the two sand habitats. Many species which occurred as one of the top ten in each habitat persisted throughout the course of the study (July, 1978 - Nov. 1979) and were characteristic of the habitat examined. Although infaunal abundances were concentrated at the sediment surface in all three habitats, the grassbed supported a larger number of individuals deeper in the sediments than did the other two habitats.

The epifaunal component of the vegetated habitat comprised a unique and diverse assemblage of species which was similar between each area investigated (i.e. *Zostera marina*, *Ruppia maritima*, and mixed stands). Few seasonal patterns in epifaunal abundance were evident in the data. Vegetated areas provided greater habitat heterogeneity and were therefore capable of supporting a greater overall diversity of species than nonvegetated habitats.

INTRODUCTION

One of the most notable features of the shallower margins along the Chesapeake Bay is the presence of submerged macrophytes in many areas. Over 8,400 hectares (20,750 acres) of the nearshore meso- and polyhaline and sublittoral zone is vegetated by Zostera marina and/or Ruppia maritima (Orth, et al. 1979). This submerged aquatic vegetation (SAV) adds a third dimension to an otherwise relatively flat sandy bottom and provides a food source, substrate and refuge for numerous species allowing for the maintenance of high faunal densities. The large stock of organisms inhabiting grassbeds is thought to be fundamental to the resource value of SAV.

Most invertebrates assimilate energy fixed by seagrasses via a detrital pathway (Fenchel, 1977; Klug, 1980). These detritivores are in turn utilized by resident and migratory consumers such as crabs, fishes and waterfowl, thereby providing an important trophic link between primary producers and species in higher trophic levels (Carr and Adams, 1973; Brook, 1975, 1977; Adams, 1976; Stoner, 1979; Stoner and Livingston, 1980; Zimmerman, 1979; Nilsson, 1969). The transfer of energy from SAV to migratory waterfowl species including swans, geese and some ducks, is more immediate through a direct consumption of the macrophytes (Verhoeven, 1978; Bayley et al., 1978; Cottam and Munro, 1954).

The biotic community within grassbeds can be quite distinct from that of unvegetated areas. The epifaunal and infaunal components are represented by a diverse and complex assemblage which includes macro- and microalgae, protozoans, nematodes and other meiofauna, hydrozoans, bryozoans, polychaetes, oligochaetes, mollusks, crustaceans and several other groups. Many species exhibit distinct seasonal pulses of abundance depending on their individual spawning periods (Stevenson and Confer, 1978).

Numerous epifaunal species are generally not found on sandy bottoms unless a suitable substrate such as large shells are present. The fact that the epifauna may not be totally dependent on the presence of grass but is able to exist on a variety of non-living substrates does not diminish the importance of seagrasses as a habitat for these species. Unlike many inert substrates, marine grasses represent a renewable resource for colonization. This quality accounts in part for the high faunal diversity and density found in grassbeds from one year to the next.

The infaunal community of grassbeds is also quite distinct from that found in adjacent unvegetated areas with substantially greater numbers of species and individuals found in vegetated areas. This increase may be related to greater sediment stability, microhabitat complexity and/or food supply (Orth, 1977; Thayer, Adams and La Croix, 1975). Orth (1977) found the infauna of a Chesapeake Bay Z. marina bed to increase in density and diversity from the edge of the bed to its center. A similar positive correlation existed with species abundance, as well as diversity, and the increasing size of the bed. He related greater faunal abundances to the sediment stabilizing function of eelgrass. Orth (1977) showed experimentally that through decreasing the stability of sediments by clipping blades of grass near the sediment surface and by simulating wave action, the density and diversity of the infauna was decreased. Natural biological disturbances such as cownose ray activity had similar affects (Orth, 1975). The vertical component provided by seagrasses which is differentiated into leaves, stems, rhizomes and roots increases microhabitat complexity and supports a greater faunal diversity than is found in unvegetated bottoms (Kikuchi 1980). Furthermore, numerous species of animals which do not feed directly on the seagrasses are thereby able to exist in such vegetated habitats (Thayer et al. 1978).

The natant community associated with SAV is diverse and quite distinct from that of surrounding unvegetated areas (Orth and Heck, 1980; Heck and Orth, 1980; Kikuchi, 1974). Many species comprising this community rely on the macrophytes during certain critical life history stages. Hardwick (1973) found that the West Coast herring, Clupea harengus pallasi, used eelgrass leaves for egg attachment. East coast species which use grassbeds in a similar manner include the halfbeak, Hyporhamphus sp. and the rough silverside, Membras martinica (John Olney, pers. comm.). The toadfish Opsanus tau uses the rhizomes as attachment sites for its eggs as well (Orth, pers. comm.). One of the more complete studies of eelgrass fish communities was conducted by Adams (1976a,b,c) in North Carolina. He found the highest fish biomass when temperature and eelgrass biomass were greatest. Further, food produced within the grassbed could have accounted for approximately 56% by weight of the diet of the fish in this community. The high fish production was due to juveniles which had higher growth efficiencies than older fishes. They accounted for 79-84% of the total annual fish production. In addition to fish, natant invertebrates such as shrimp and blue crabs are found in considerably greater abundance as both juveniles and adults in eelgrass beds than in sandy habitats (Lippson, 1970; Heck and Orth, 1980). Changes in eelgrass abundance are even thought to cause variations in the commercial catch of blue crabs. Thus, it appears that grassbeds provide numerous advantages to a variety of species and constitute a valuable natural resource in the Chesapeake Bay.

In addition to the biological benefits provided by submerged macrophytes, the plants serve other functional roles such as buffering erosion by trapping sands and pumping nutrients from the sediments to the leaves and eventually to the water column. These functions are generally not achieved by artificial substrates which further emphasizes the importance of SAV in the marine environment.

When studying the dynamics of a particular habitat, a knowledge of both the structural complexity and functional aspects of the system are desirable. Both serve as a means for evaluating the habitat for management purposes, particularly if other habitats have been similarly studied so that comparative data are available. The objective of this section is to compare the macroinvertebrate assemblages associated with the different habitat types found at the Vaucluse Shores study site. These include the grassbed proper (eelgrass, widgeongrass, and mixed vegetation), inshore unvegetated sand patches within the grassbed, and an offshore series of sand bars and troughs which separate the vegetated area from the deeper waters of the Chesapeake Bay.

METHODS AND MATERIALS

Routine sampling was scheduled to coincide with major biological events in the grassbed and adjacent areas. These events included the arrival of major predators in the system (early spring), the partial defoliation of *Z. marina* (mid-summer), and the predominant larval settling periods (spring and fall). Such timing, rather than quarterly sampling, would yield the best data on the structural characterization of the grass bed and adjacent habitats.

Three habitats (Fig. 1) were sampled six times (July and October, 1978 and April, June and September and November, 1979) to determine quantitative and qualitative differences in their associated fauna. The habitats included an offshore sandbar system (outside sand or OS), sandy patches within the grass bed (inside sand or IS) and the grass bed (G) proper (Fig. 1). Vegetated areas included an inshore *Ruppia maritima* zone, a *Zostera marina* zone offshore and a mixed stand of vegetation in between. Samples were considered to be from the mixed area if the least abundant plant species comprised a minimum of 15% of the total vegetational dry weight biomass in the sample.

Initially, 10 stations were established in each habitat. However, data analysis from the first sampling indicated that 5 rather than 10 stations adequately represented the infauna in each of the two sand habitats. One sediment (3.8 cm^2) and three macroinfaunal (0.007 m^2 each) cores were taken at each station. Prior to taking infaunal and sediment cores in the grass bed an epifaunal sample was taken at each station by clipping and collecting grass from the area to be sampled. Coring was then conducted within the clipped area. Coring was chosen as the appropriate sampling method because the root and rhizome mat in the grassbed made sampling with other devices difficult. In order to maintain gear comparability, identical cores were used in unvegetated habitats. All samples were taken while diving with SCUBA.

Vertical distribution of infauna was examined in July 1978. A 35 cm long plexiglass core 9.4 cm in diameter (0.007 m^2) was used to collect infaunal samples. One such core sample was taken at each station. The top 10 cm of each sample was sectioned vertically into 2 cm intervals and the remaining material was divided into 5 cm intervals. Based on these data, it was determined that a sample depth of 15 cm adequately collected the infauna.

Before sieving and preservation samples were held for at least 30 min. in labelled plastic bags containing isotonic $MgCl_2$ as a relaxant. This kept many of the smaller polychaetes and oligochaetes from fragmenting and/or crawling through the sieve. All infaunal samples were washed through 0.5 mm mesh sieves and the retained material was preserved in 10% buffered seawater formalin. A vital stain (Rose Bengal) was added to facilitate laboratory sorting. All invertebrates in each sample were removed from the remaining

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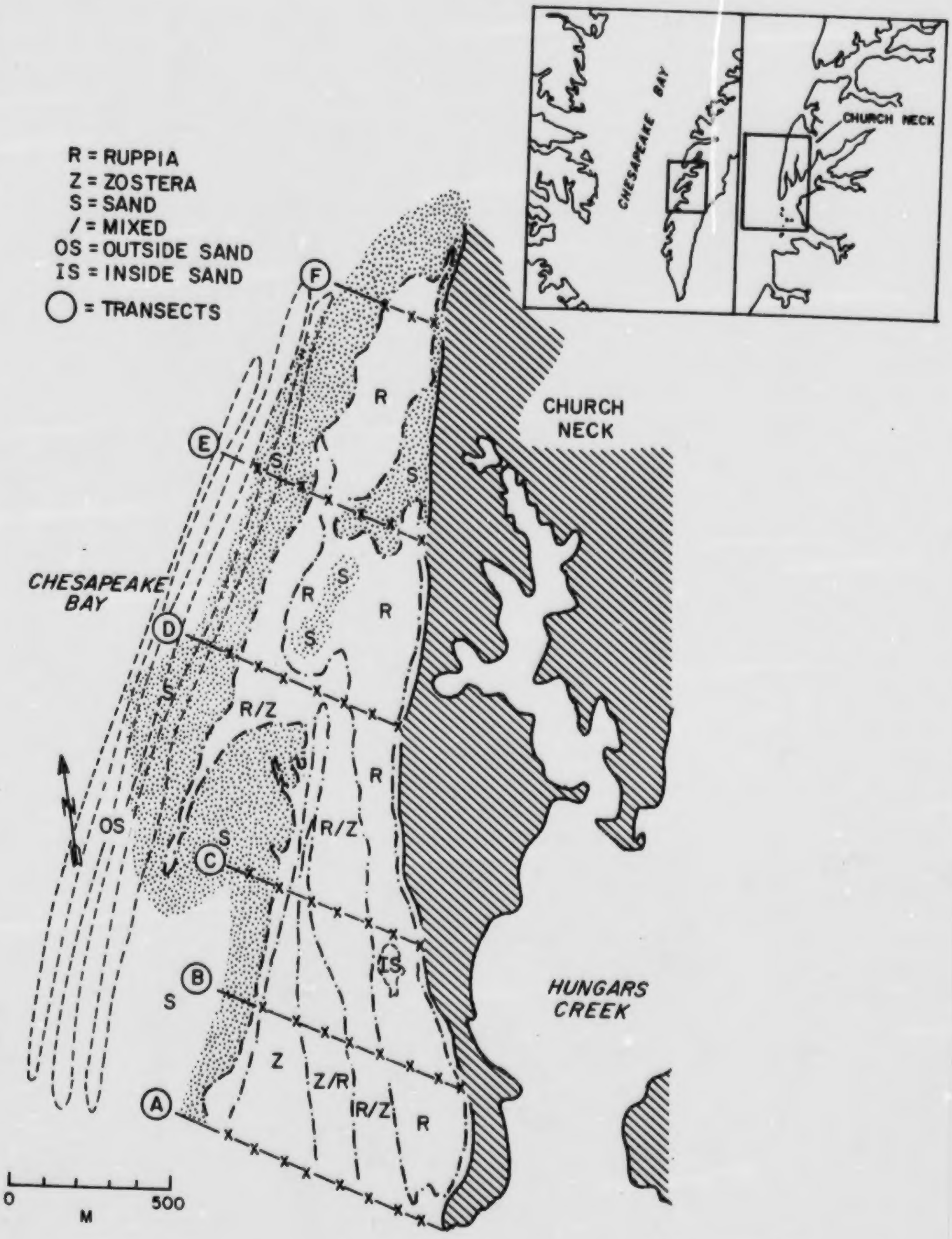
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Z = ZOSTERA
S = SAND
/ = MIXED
OS = OUTSIDE SAND
IS = INSIDE SAND
○ = TRANSECTS
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CHURCH NECK
CHESAPEAKE BAY
CHURCH NECK
HUNGARS CREEK
A
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Fig. 1. Study site showing vegetation zones, the inside sand station (IS) and the outside sand station (OS).

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sediments and associated plant debris using forceps while microscopically examining spoonfulls of each sample placed in a petri dish.

Epifaunal samples were collected by clipping plants to within 2-3 cm of the sediment surface and easing the blades into a collecting bag with a 0.5 mm mesh bottom (Marsh 1973). Samples were kept in water and processed live by stripping all epifauna from the blades and preserving them in 10% buffered seawater formalin containing the vital stain Rose Bengal. The remaining plant material was sorted to species (*Ruppia*, *Zostera* and algae), oven-dried at 80°C for at least 48 h and then weighed to the nearest 0.1 g.

Numerical abundance histograms were plotted by area for both species and individuals found in the infaunal and epifaunal (grassbed only) community. Species diversity was calculated for each area using the index of Shannon (Pielou, 1975). The index H' is expressed as:

$$H' = \sum_{i=1}^{s} Pi \log_2 Pi$$

where s = number of species in the sample and Pi = proportion of the i-th species in the sample. This index is commonly used for comparative purposes and includes both a species richness (the number of species in a community) component and an evenness (how equitably the individuals are distributed between the species) component.

RESULTS

Cumulative species curves for vertically sectioned cores taken in each habitat approached a plateau after the number of species from the top 15 cm of sediment had been plotted (Fig. 2). Although most species in each habitat were found in the top 15 cm of sediment, the composition and numbers of individuals of the dominant taxa differed from one area to the next (Table 1). Infaunal abundances were concentrated at the sediment surface in all three habitats, but the grassbed supported a larger number of individuals deeper in the sediments than did the other two habitats (Table 1).

Generally infaunal species means per core were twice as great for vegetated areas as those for unvegetated habitats (Fig. 3). Samples from the sandy habitat had a mean of between 4 and 11 species per core whereas means for vegetated areas ranged from 14 to 30 species per core. With the exception of the September and November, 1979 sample dates, the number of infaunal species of the inside sand habitats showed slightly higher abundance than the more dynamic offshore sand habitat. Within the three vegetated areas (*Ruppia*, *Zostera*, and mixed) fewer species were usually associated with *Ruppia* than were found in the *Zostera* or mixed zones.

Seasonal trends in species abundances were not readily apparent. Mean numbers of species per core were depressed in all habitats during September, 1979. Otherwise, distinct seasonal pulses in species abundances were obscure.

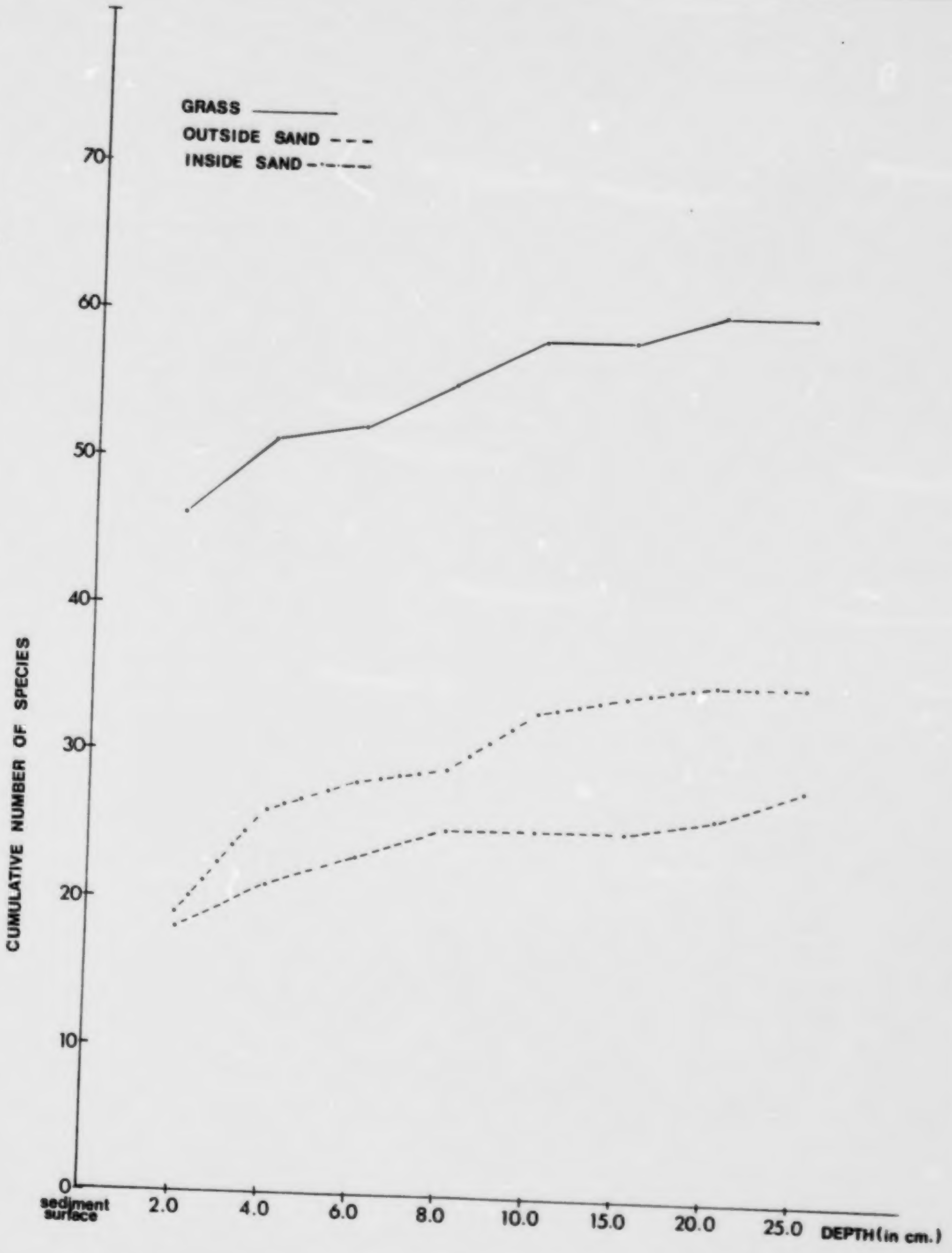

Fig. 2. Cumulative species curves of vertically sectioned cores from three habitats.

TABLE 1. VERTICAL DISTRIBUTION IN NUMBERS PER CORE (70 cm^2) OF DOMINANT INFAUNA BY HABITAT

	Grassbed Proper		Dynamic Sand Bar Area		Sand Patches Within Grassbed	
Sediment Surface						
	Polydora ligni	384	*Gemma gemma*	42	*Gemma gemma*	1,931
	Heteromastus filiformis	204	*Neomysis americana*	11	*Odostomia* sp.	726
	Nereis succinea	79	*Scolelepis squamata*	6	*Mya arenaria*	7
	Streblospio benedicti	75			*Brania clavata*	5
	Erichsonella attenuata	71			*Glycinde solitaria*	5
2.0 cm						
	Heteromastus filiformis	160	*Scolelepis squamata*	7	*Gemma gemma*	30
	Oligochaeta	54			*Odostomia* sp.	27
	Polydora ligni	22			*Scolelepis squamata*	8
4.0 cm						
	Heteromastus filiformis	107	*Glycera dibranchiata*	5	*Heteromastus filiformis*	19
	Oligochaeta	25			*Chaetazone setosa*	9
	Polydora ligni	22			*Scolelepis squamata*	6
6.0 cm						
	Heteromastus filiformis	63	*Paraonis fulgens*	4	*Heteromastus filiformis*	20
	Oligochaeta	37	*Spiophanes bombyx*	3	*Chaetazone setosa*	4
	Polydora ligni	6	*Glycera dibranchiata*	2	*Spiophanes bombyx*	2
8.0 cm						
	Oligochaeta	60	*Spiophanes bombyx*	11	*Heteromastus filiformis*	11
	Heteromastus filiformis	28	*Paraonis fulgens*	4	*Glycera dibranchiata*	2
	Glycera dibranchiata	4				
10.0 cm						
	Oligochaeta	163	*Spiophanes bombyx*	3	*Heteromastus filiformis*	11
	Heteromastus filiformis	18	*Glycera dibranchiata*	2	*Glycera dibranchiata*	2
	Pseudoeurythoe ambigua	7			Oligochaeta	2
15.0 cm						
	Oligochaeta	16	*Spiophanes bombyx*	4	Oligochaeta	2
	Pseudoeurythoe ambigua	7	*Paraonis fulgens*	4	*Heteromastus filiformis*	1
	Heteromastus filiformis	5				
20.0 cm						
	Oligochaeta	9	*Glycera dibranchiata*	2	*Heteromastus filiformis*	5
	Heteromastus filiformis	4	*Eteone heteropoda*	1	Oligochaeta	3
	Polydora ligni	2				
25.0 cm						

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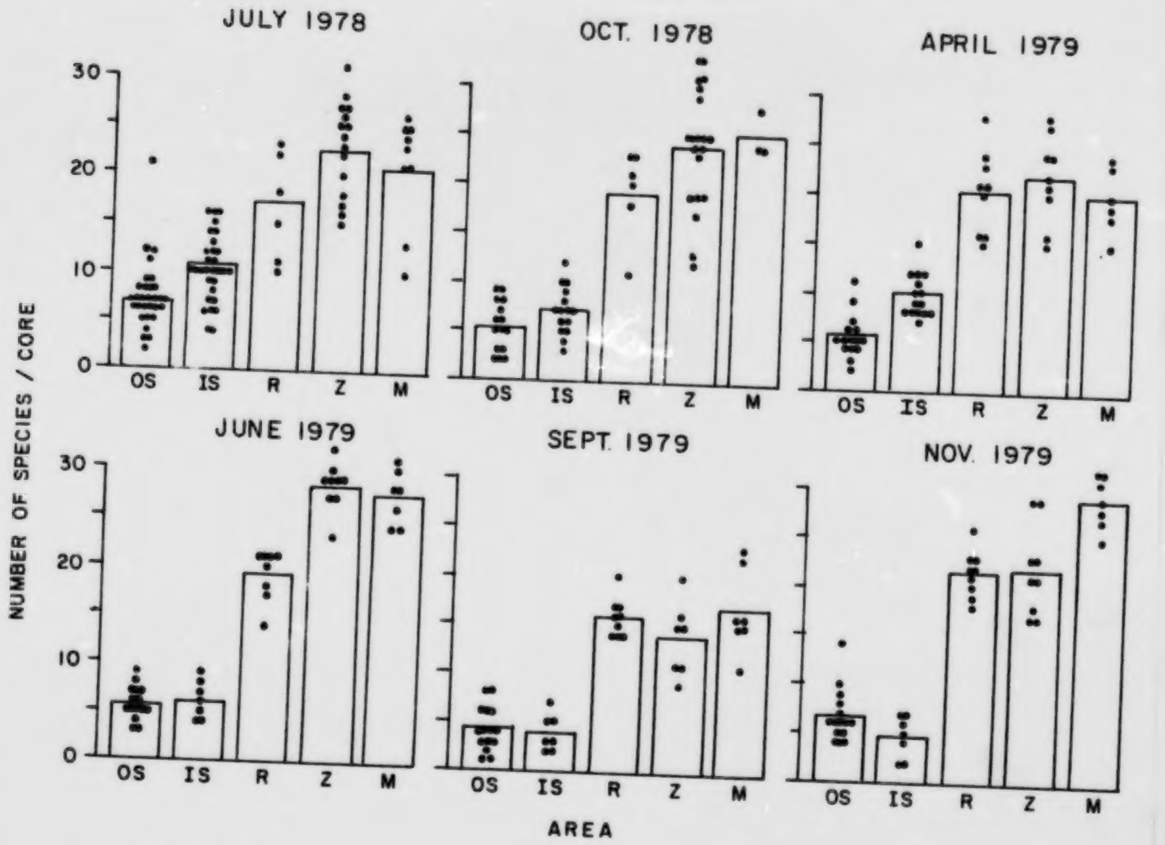

Fig. 3. Number of infaunal species per core (0.007 m^2) found in each habitat. Treatment designations are as follows: OS = outside sand; IS = inside sand; R = *Ruppia maritima*; Z = *Zostera marina*; M = mixed vegetation. Closed circles indicate the number of individuals for each core. Boxes represent the mean number of individuals per core for each area.

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The mean number of infaunal individuals per core generally followed the trends seen for species, with those in the sandy area being lower than those from the vegetated bottom (Fig. 4). One exception occurred in July, 1978, when densities of individuals ($\bar{x}$ of about 300 per core) at the inside sand stations exceeded that found in any other habitat. Typically, samples had means of around 20 individuals per core and in all but the least two sample periods, data from the inside sand habitat showed a greater mean abundance of individuals than that from the more dynamic sand bar area. In general, the range in numbers of individuals per core in the nonvegetated areas was greater than that for the grassbed as evidenced by the wider scatter of individual sample data points. This implies that the sand-associated fauna were more patchily distributed than the grassbed fauna.

There was no consistent pattern for mean infaunal individual abundances between the three vegetated areas (Fig. 4). On July and October, 1978 and November 1979, the greatest number of individuals were found in the mixed habitat whereas the Ruppia zone showed greatest abundances in April and September 1979.

Seasonal trends in the number of individuals were clearly evident in the vegetated area (Fig. 4). Mean abundances (between 500 to 1000) were considerably increased during April 1979 with the lowest means evident the following September (between 50 and 110). The months of October and September showed the lowest mean abundances of individuals from 1978 and 1979 with between 100-200 and 50-110 individuals, respectively.

Mean species diversities (Shannon H') for the infauna varied widely over the study period ranging from 1.6 to 2.2 in the outside sand area; 1.4 to 2.7 in the inside sand habitat; and 2.0 to 3.7 in the grassbed (Fig. 5). In general diversities were higher in the grassbed than in the nonvegetated areas. No consistent patterns in species diversity were seen between either the two sandy habitats or between the three vegetated zones.

An examination of the top ten infaunal species in each habitat for the six sample dates (Tables 2-7) shows that these species comprised between 77% (Zostera 10/78) and 98% (IS 7/78) of the total community. Each habitat had several species which persisted through time as one of the top ten species. In many cases these species were locally common to each of the habitats examined. For example, the small bivalve, Gemma gemma was consistently abundant in both the sandy habitats and occurred sporadically in both the Ruppia and mixed zones but was overshadowed by other numerically abundant species in the Zostera area. The polychaete Scolelepis squamata generally persisted as one of the top ten species in both unvegetated habitats although it was more regularly found in the inside sand area. Heteromastis filiformis (Polychaeta) and Oligochaeta spp. were consistently abundant in the IS habitat as well as in all three vegetated sediments but not at the dynamic OS stations. The inside sand (IS) stations were characterized by the parasitic gastropod Odostomia spp. Acanthohaustorius millsi, a burrowing amphipod, was found only in the OS samples. Species which characterized the vegetated habitats included the errant polychaete Nereis succinea, the generally epibenthic isopod, Edotea triloba, and several species which are common in the

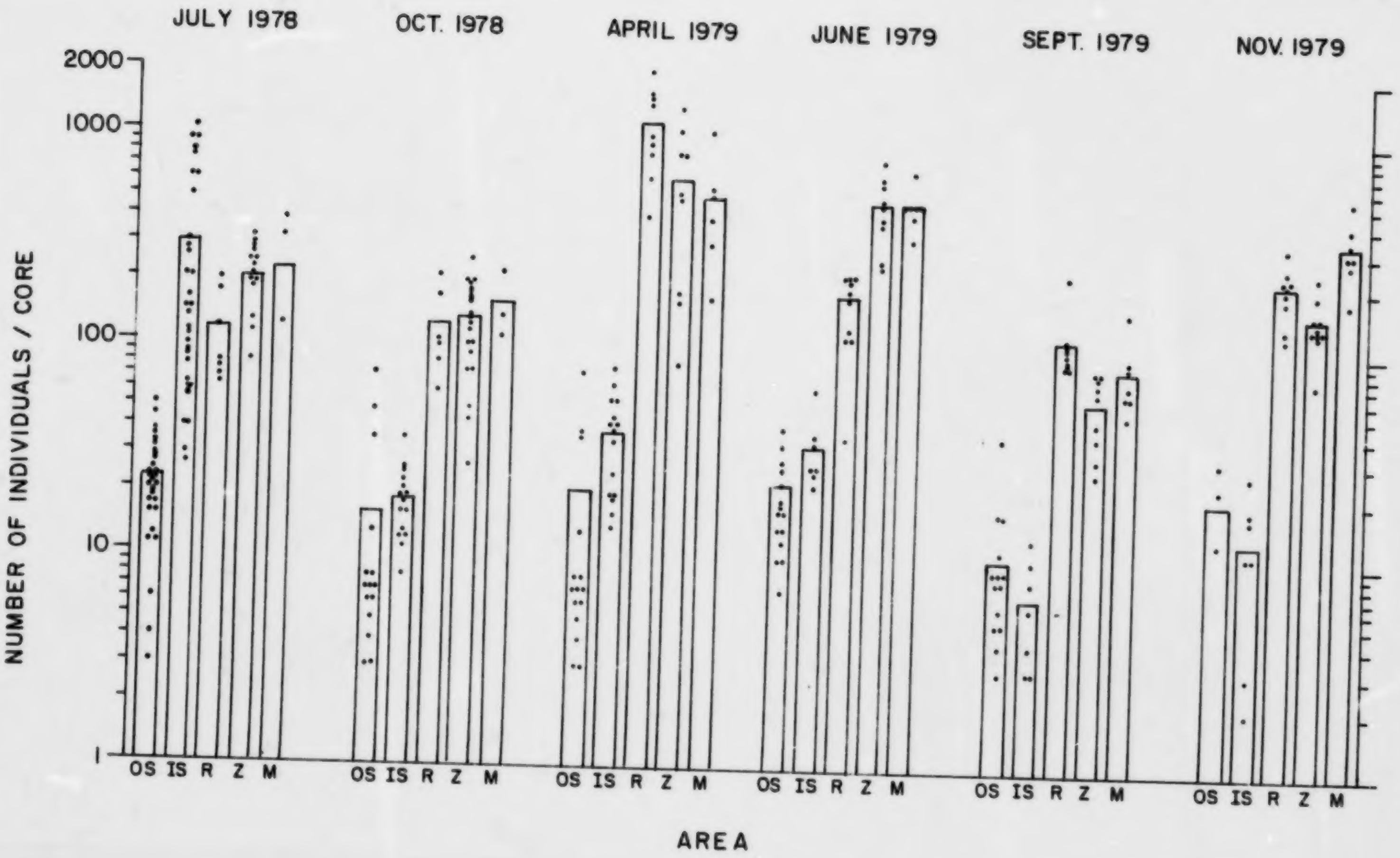

Fig. 4. Infaunal abundance expressed as the number of individuals per core (0.007 m^2) found in each habitat. Treatment designations are as follows: OS = outside sand; IS = inside sand; R = *Ruppia maritima*; Z =*Zostera marina*; M = mixed vegetation. Closed circles indicate the number of individuals for each core. Boxes represent the mean number of individuals per core for each area.

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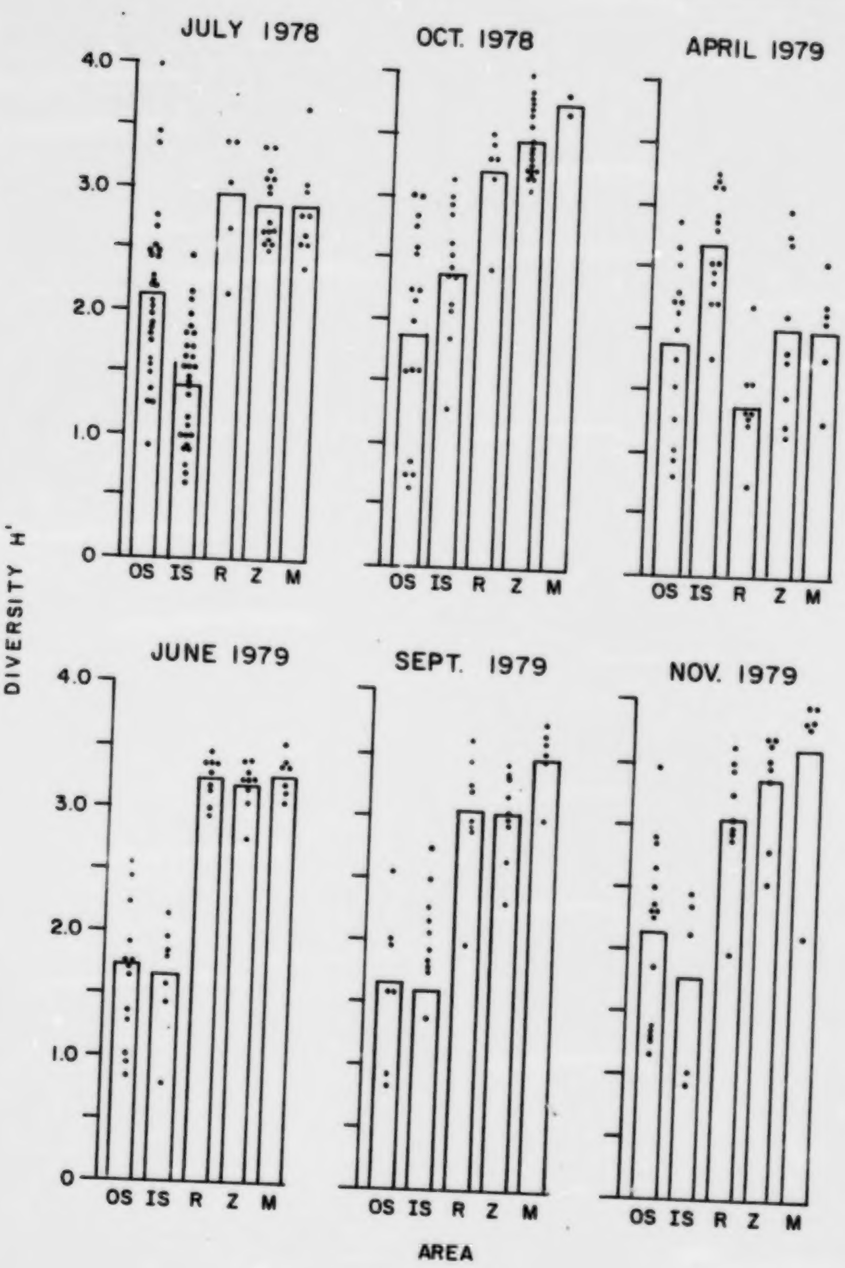

Fig. 5. Infaunal species diversity (Shannon H') for each habitat. Treatment designations are as follows: OS = outside sand; IS = inside sand; R = *Ruppia maritima*; Z = *Zostera marina*; M = mixed vegetation. Closed circles indicate the diversity for each core. Boxes represent the mean diversity for each area.

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TABLE 2. INFAUNAL SPECIES RECORDED IN THE SAND AND GRASS HABITATS OF VAUCLUSE SHORE ON JULY, 1978.

Inside Sand

Species	°/o	#/m^2
1. *Gemma gemma*	77.74	33115.96
2. *Odostomia*	13.59	5787.44
3. *Heteromastus filiformis*	2.76	1173.91
4. *Oligochaeta*	1.33	565.22
5. *Odostomia bisuturalis*	.77	328.50
6. *Scolelepis squamata*	.67	285.02
7. *Tharyx setigera*	.66	280.19
8. *Spiophanes bombyx*	.26	111.11
9. *Turbellaria*	.19	82.13
10. *Scolecolepides viridis*	.18	77.29
Totals	98.15	41806.77
Total sample	100.00	42598.80

OUTSIDE SAND

Species	°/o	#/m^2
1. *Gemma gemma*	33.38	1096.62
2. *Spiophanes bombyx*	15.29	502.42
3. *Paraonis fulgens*	13.09	429.95
4. *Scolelepis squamata*	8.09	265.70
5. *Glycera dibranchiata*	7.35	241.55
6. *Scoloplos*	3.09	101.45
7. *Acanthohaustorius millsi*	3.09	101.45
8. *Mulinia lateralis*	1.76	57.97
9. *Neomysis americana*	1.62	53.14
10. *Chaetozone* Sp A	1.18	38.65
Totals	87.94	2888.90
Total sample	100.00	3285.01

RUPPIA

Species	°/o	#/m^2
1. *Heteromastus filiformis*	30.91	5144.93
2. *Polydora ligni*	14.22	2367.15
3. *Nereis succinea*	10.16	1690.82
4. *Oligochaeta*	9.26	1545.89
5. *Gemma gemma*	6.53	1086.96
6. *Erichsonella attenuata*	6.10	1014.49
7. *Edotea triloba*	3.77	628.02
8. *Streblospio benedicti*	2.03	338.16
9. *Microprotopus raneyi*	1.74	289.85
10. *Gammarus mucronatus*	1.60	265.70
Totals	86.32	14371.97
Total sample	100.00	16642.51

ZOSTERA

Species	°/o	#/m^2
1. *Heteromastus filiformis*	34.34	10106.29
2. *Oligochaeta*	18.59	5468.60
3. *Polydora ligni*	16.49	4850.24
4. *Streblospio benedicti*	6.27	1845.41
5. *Nereis succinea*	4.04	1188.41
6. *Edotea triloba*	1.97	579.71
7. *Pseudeurythoe ambigua*	1.74	512.08
8. *Erichsonella attenuata*	1.18	347.83
9. *Crepidula convexa*	1.08	318.84
10. *Glycera ditranchiata*	0.99	289.85
Totals	86.69	25507.26
Total sample	100.00	29410.63

MIXED

Species	°/o	#/m^2
1. *Heteromastus filiformis*	33.07	10676.33
2. *Polydora ligni*	23.34	7536.23
3. *Oligochaeta*	9.88	3188.41
4. *Streblospio benedicti*	7.13	2302.74
5. *Nereis succinea*	5.24	1690.82
6. *Erichsonella attenuata*	3.84	1239.94
7. *Edotea triloba*	2.34	756.84
8. *Tharyx setigera*	1.45	466.99
9. *Gemma gemma*	1.45	466.99
10. *Mya arenaria*	1.30	418.68
Totals	89.04	28743.97
Total sample	100.00	32286.64

TABLE 3. INFAUNAL SPECIES RECORDED IN THE SAND AND GRASS HABITATS AT VAUCLUSE SHORE ON OCTOBER 1978.

INSIDE SAND

Species	°/o	#/m^2
1. Capitella capitata	25.45	676.33
2. Scolelepis squamata	21.45	570.05
3. Heteromastus filiformis	12.36	328.50
4. Gemma gemma	11.46	309.18
5. Mysidopsis bigelowi	4.00	106.28
6. Spiophanes bombyx	3.64	96.62
7. Glycinde solitaria	3.27	86.98
8. Odostomia	2.18	57.97
9. Oligochaeta	1.82	48.31
10. Gastropoda	1.82	48.31
Totals	87.63	2328.51
Total sample	100.00	2657.00

OUTSIDE SAND

Species	°/o	#/m^2
1. Paraonis fulgens	54.24	1236.72
2. Gemma gemma	11.02	251.21
3. Scoloplos	4.66	106.28
4. Neomysis americana	3.81	86.96
5. Glycinde solitaria	2.54	57.97
6. Scolelepis squamata	2.12	48.31
7. Acanthohaustorius millsi	2.12	48.31
8. Microprotopus raneyi	2.12	48.31
9. Cymadusa compta	2.12	48.31
10. Rhynchocoela	1.27	28.99
Totals	86.02	1961.37
Total sample	100.00	2280.19

RUPPIA

Species	°/o	#/m^2
1. Heteromastus filiformis	20.54	3671.50
2. Polydora ligni	19.46	3478.26
3. Hargeria rapax	13.51	2415.46
4. Nereis succinea	10.14	1811.59
5. Erichsonella attenuata	7.97	1425.12
6. Cymadusa compta	5.27	942.03
7. Gemma gemma	3.51	628.02
8. Edotea triloba	2.84	507.25
9. Paracaprella tenuis	2.30	410.63
10. Microprotopus raneyi	2.03	362.32
Totals	87.57	15662.18
Total sample	100.00	17874.40

ZOSTERA

Species	°/o	#m/^{2}
1. Oligochaeta	34.68	6673.57
2. Heteromastus filiformis	10.26	1973.78
3. Spiochaetopterus oculatus	8.21	1580.40
4. Nereis succinea	4.91	945.48
5. Polydora ligni	4.05	779.85
6. Brania clavata	3.19	614.22
7. Crepidula convexa	3.16	607.32
8. Gyptis vittata	3.08	593.51
9. Microprotopus raneyi	3.01	579.71
10. Anadara tramversa	2.98	572.81
Totals	77.53	14920.65
Total sample	100.00	19240.85

MIXED

Species	°/o	#/m^2
1. Erichsonella attenuata	20.21	4589.37
2. Heteromastus filiformis	14.68	3333.33
3. Edotea triloba	9.57	2173.91
4. Nereis succinea	7.87	1787.44
5. Oligochaeta	7.23	1642.51
6. Microprotopus raneyi	5.53	1256.04
7. Spiochaetopterus oculatus	4.47	1014.49
8. Cymadusa compta	4.47	1014.49
9. Polydora ligni	4.04	917.87
10. Mollusca	2.55	597.71
Totals	80.62	18327.16
Total sample	100.00	22705.32

TABLE 4. INFAUNAL SPECIES RECORDED IN THE SAND AND GRASS HABITATS OF VAUCLUSE SHORES ON APRIL 1979.

INSIDE SAND			OUTSIDE SAND			RUPPIA		
Species	°/o	#/m²	Species	°/o	#/m²	Species	°/o	#/m²
1. Polydora ligni	25.17	1400.97	1. Paraonis fulgens	45.60	1352.66	1. Polydora ligni	77.39	130789.06
2. Scolecolepides viridis	15.97	888.89	2. Polydora ligni	7.82	231.88	2. Oligochaeta	12.12	20483.10
3. Oligochaeta	12.15	676.33	3. Scoloplos	7.82	231.88	3. Heteromastus filiformis	2.86	4830.92
4. Scolelepis squamata	10.76	599.03	4. Scolecolepides viridis	7.49	222.22	4. Nereis succinea	1.91	3220.61
5. Gemma gemma	9.55	531.40	5. Acanthohaustorius millsi	5.86	173.91	5. Brania clavata	1.26	2125.60
6. Tharyx setigera	3.13	173.91	6. Gemma gemma	3.58	106.28	6. Mediomastus ambiseta	1.03	1739.13
7. Brania clavata	2.60	144.93	7. Oligochaeta	3.26	96.62	7. Edotea triloba	0.38	644.12
8. Hargeria rapax	2.60	144.93	8. Pseudohaustorius sp. 1	3.26	96.62	8. Scoloplos	0.35	595.81
9. Heteromastus filiformis	2.26	125.60	9. Saccoglossus kowalewskii	2.61	77.29	9. Gastropoda	0.31	531.40
10. Saccoglossus	1.91	106.28	10. Parahaustorius longimerus	2.61	77.29	10. Capitella sp. 3 seta	0.27	450.89
Totals	86.10	4792.27	Totals	89.91	2666.65	Totals	97.88	165410.64
Total sample	100.00	5565.21	Total sample	100.00	2966.18	Total sample	100.00	169001.56

ZOSTERA			MIXED		
Species	°/o	#/m²	Species	°/o	#/m²
1. Polydora ligni	72.44	65265.72	1. Polydora ligni	61.84	46497.60
2. Oligochaeta	12.33	11111.11	2. Oligochaeta	18.57	13961.36
3. Heteromastus filiformis	3.31	2979.07	3. Heteromastus filiformis	4.56	3429.95
4. Gammarus mucronatus	1.55	1400.97	4. Nereis succinea	4.11	3091.79
5. Brania clavata	1.35	1223.83	5. Mediomastus ambiseta	1.38	1038.65
6. Nereis succinea	1.36	1223.83	6. Scoloplos	1.16	869.57
7. Gyptis vittata	1.36	1223.83	7. Gemma gemma	1.00	748.79
8. Mediomastus ambiseta	1.11	998.39	8. Brania clavata	0.96	724.64
9. Scoloplos	0.80	724.64	9. Gammarus mucronatus	0.93	724.64
10. Spio setosa	0.55	499.19	10. Scoleolepides viridis	0.87	652.17
Totals	95.38	85942.05	Totals	95.38	71715.00
Total sample	100.00	90096.56	Total sample	100.00	75193.19

TABLE 5. INFAUNAL SPECIES RECORDED IN THE SAND AND GRASS HABITATS OF VAUCLUSE SHORES ON JUNE, 1979.

INSIDE SAND

Species	°/o	#/m²
1. *Gemma gemma*	57.02	2857.14
2. *Oligochaeta*	14.05	703.93
3. *Scolecolepides viridis*	7.85	393.37
4. *Capitella capitata*	4.55	227.74
5. *Heteromastus filiformis*	3.72	186.34
6. *Scolelepis squamata*	3.31	165.63
7. *Mya arenaria*	2.89	144.93
8. *Gastropoda*	1.65	82.82
9. *Haminoea solitaria*	1.24	62.11
10. *Polydora ligni*	0.83	41.41
Totals	97.11	4865.42
Total sample	100.00	5010.35

OUTSIDE SAND

Species	°/o	#/m²
1. *Paraonis fulgens*	44.08	1294.69
2. *Gemma gemma*	15.79	463.77
3. *Acanthohaustorius millsi*	11.18	328.50
4. *Scoloplos*	4.93	144.93
5. *Glycera dibranchiata*	3.95	115.94
6. *Mulinia lateralis*	3.95	115.94
7. *Spiophanes bombyx*	1.97	57.97
8. *Chiridotea caeca*	1.64	48.31
9. *Parahaustorius longimerus*	1.64	48.31
10. *Scolelepis squamata*	1.32	38.65
Totals	89.13	2657.01
Total sample	100.00	2937.19

RUPPIA

Species	°/o	#/m²
1. *Heteromastus filiformis*	21.64	5603.86
2. *Balanus improvisus*	20.09	5201.29
3. *Polydora ligni*	13.31	3446.06
4. *Gemma gemma*	11.69	3027.38
5. *Nereis succinea*	5.10	1320.45
6. *Oligochaeta*	4.04	1046.70
7. *Streblospio benedicti*	3.92	1014.49
8. *Tharyx setigera*	3.54	917.87
9. *Erichsonella attenuata*	3.11	805.15
10. *Edotea triloba*	2.86	740.74
Totals	89.30	23123.99
Total sample	100.00	25893.72

ZOSTERA

Species	°/o	#/m²
1. *Balanus improvisus*	23.10	16376.82
2. *Heteromastus filiformis*	22.39	15877.62
3. *Polydora ligni*	22.19	15732.69
4. *Streblospio benedicti*	4.66	3301.13
5. *Oligochaeta*	4.50	2898.55
6. *Mya arenaria*	4.09	2898.55
7. *Nereis succinea*	4.07	2882.45
8. *Cistena gouldii*	1.82	1288.25
9. *Sabellaria vulgaris*	1.79	1272.14
10. *Microprotopus raneyi*	1.14	805.15
Totals	89.75	63623.21
Total sample	100.00	70901.69

MIXED

Species	°/o	#/m²
1. *Heteromastus filiformis*	27.94	20041.41
2. *Balanus improvisus*	24.16	17329.20
3. *Oligochaeta*	8.72	6252.59
4. *Polydora ligni*	8.00	5734.99
5. *Streblospio benedicti*	6.44	4616.98
6. *Nereis succinea*	4.01	2877.85
7. *Gemma gemma*	3.26	2239.55
8. *Edotea triloba*	2.60	1863.35
9. *Erichsonella attenuata*	2.48	1780.54
10. *Mya arenaria*	2.45	1759.83
Totals	90.06	64596.29
Total sample	100.00	71718.38

TABLE 6. INFAUNAL SPECIES RECORDED IN THE SAND AND GRASS HABITATS OF VAUCLUSE SHORES ON SEPTEMBER 1979.

INSIDE SAND

Species	$^o/_o$	#/m^2
1. Capitella capitata	40.43	393.37
2. Heteromastus filiformis	14.89	144.93
3. Oligochaeta	8.51	82.82
4. Scolelepis squamata	6.38	62.11
5. Streblospio benedicti	6.38	62.11
6. Ampithoe longimana	6.38	62.11
7. Paraprionospio pinnata	4.26	41.41
8. Glycinde solitaria	2.13	20.70
9. Polydora ligni	2.13	20.70
10. Scolecolepides viridis	2.13	20.70
Totals	93.62	910.96
Total sample	100.00	973.08

OUTSIDE SAND

Species	$^o/_o$	#/m^2
1. Paraonis fulgens	24.00	347.83
2. Scoloplos	22.00	318.84
3. Neomysis americana	16.00	231.88
4. Gemma gemma	6.67	96.62
5. Retusa canaliculata	5.33	77.29
6. Acanthohaustorius millsi	5.33	77.29
7. Glycera dibranchiata	4.00	57.97
8. Scolelepis squamata	3.33	48.31
9. Protohaustorius deichmannae	3.73	48.31
10. Rhynchocoela	2.67	38.65
Totals	92.66	1342.99
Total sample	100.00	1449.28

RUPPIA

Species	$^o/_o$	#/m^2
1. Erichsonella attenuata	20.33	3349.44
2. Oligochaeta	19.06	3140.10
3. Nereis succinea	15.74	2592.59
4. Heteromastus filiformis	10.07	1658.62
5. Gemma gemma	8.02	1320.45
6. Hargeria rapax	5.47	901.77
7. Edotea triloba	5.08	837.36
8. Cymadusa compta	3.62	595.81
9. Polydora ligni	2.74	450.89
10. Balanus improvisus	1.86	305.96
Totals	91.99	15152.99
Total sample	100.00	16473.43

ZOSTERA

Species	$^o/_o$	#/m^2
1. Heteromastus filiformis	28.54	2399.36
2. Oligochaeta	19.54	1642.51
3. Nereis succinea	10.73	901.77
4. Spiochaetopterus oculatus	10.34	869.57
5. Crepidula convexa	3.45	289.85
6. Erichsonella attenuata	3.07	257.65
7. Edotea triloba	2.87	241.55
8. Cymadusa compta	2.87	241.55
9. Scolopolos	2.49	209.34
10. Gammarus mucronatus	1.53	128.82
Totals	85.43	7181.97
Total sample	100.00	8405.80

MIXED

Species	$^o/_o$	#/m^2
1. Nereis succinea	19.17	2298.14
2. Gemma gemma	15.54	1863.35
3. Oligochaeta	10.36	1242.24
4. Erichsonella attenuata	8.12	973.09
5. Heteromastus filiformis	7.43	890.27
6. Cymadusa compta	6.56	786.75
7. Spiochaetopterus oculatus	4.66	559.01
8. Edotea triloba	4.32	517.60
9. Crepidula convexa	3.45	414.08
10. Scoloplos	3.28	393.37
Totals	82.89	9937.90
Total sample	100.00	11987.58

TABLE 7. INFAUNAL SPECIES RECORDED IN THE SAND AND GRASS HABITATS OF VAUCLUSE SHORES ON NOVEMBER 1979.

INSIDE SAND

Species	°/o	#/m^2
1. Capitella capitata	42.70	786.75
2. Gemma gemma	17.98	331.26
3. Streblospio benedicti	11.24	207.04
4. Scolelepis squamata	7.87	144.93
5. Rhynchocoela	5.62	103.52
6. Heteromastus filiformis	5.62	103.52
7. Hargeria rapax	3.37	62.11
8. Spiochaetopterus oculatus	1.12	20.70
9. Retusa canaliculata	1.12	20.70
10. Neomysis americana	1.12	20.70
Totals	97.76	1801.23
Total sample	100.00	1842.65

OUTSIDE SAND

Species	°/o	#/m^2
1. Paraonis fulgens	41.75	1198.07
2. Scoloplos	17.57	502.42
3. Gemma gemma	9.43	270.53
4. Acanthohaustorius millsi	8.08	231.88
5. Scolelepis squamata	4.71	135.27
6. Spiophanes bombyx	2.02	57.97
7. Retusa canaliculata	1.35	38.65
8. Saccoglossus kowalewskii	1.35	38.65
9. Pseudoleptocuma minor	1.35	38.65
10. Mysidopsis bigelowi	1.01	28.99
Totals	88.56	2541.08
Total sample	100.00	2869.56

RUPPIA

Species	°/o	#/m^2
1. Polydora ligni	22.30	7085.35
2. Oligochaeta	18.04	5732.69
3. Nereis succinea	14.39	4573.27
4. Heteromastus filiformis	8.21	2608.70
5. Erichsonella attenuata	6.94	2206.12
6. Hargeria rapax	4.11	1304.35
7. Gemma gemma	4.00	1272.14
8. Ampeliscidae	3.90	1239.94
9. Streblospio benedicti	3.09	982.29
10. Edotea triloba	2.53	805.15
Totals	87.51	27810.00
Total sample	100.00	31771.34

ZOSTERA

Species	°/o	#/m^2
1. Crepidula convexa	24.35	5442.84
2. Polydora ligni	13.33	2979.07
3. Oligochaeta	10.95	2447.67
4. Mediomastus ambiseta	8.43	1884.06
5. Spiochaetopterus oculatus	8.36	1867.96
6. Heteromastus filiformis	6.12	1368.76
7. Nereis succinea	4.90	1095.01
8. Edotea triloba	4.03	901.77
9. Pseudeurythoe paucibranchiata	3.17	708.53
10. Anadara transversa	1.59	354.27
Totals	85.23	19049.94
Total sample	100.00	22351.05

MIXED

Species	°/o	#/m^2
1. Oligochaeta	28.55	14409.94
2. Polydora ligni	14.89	7515.53
3. Nereis succinea	9.60	4844.72
4. Mediomastus ambiseta	6.81	3436.85
5. Crepidula convexa	5.82	2939.96
6. Heteromastus filiformis	4.18	2111.80
7. Brania clavata	3.90	1966.87
8. Gemma gemma	3.69	1863.35
9. Streblospi benedicti	3.12	1573.50
10. Spiochaetopterus oculatus	2.87	1449.28
Totals	83.43	42111.80
Total sample	100.00	50476.16

epifaunal community such as *Polydora ligni*, *Streblospio benedicti* (Polychaeta) and the isopod, *Erichsonella attenuata*.

The epifaunal component of the vegetated habitat comprised a somewhat unique assemblage of species. Only one epifaunal clip was made in the mixed area on October 1978, and June, September and November, 1979. Therefore these histograms represent single point data and do not indicate mean abundances as indicated in other histograms. With this fact in mind, some comparisons between epifaunal communities can be made.

The largest mean number of species per grass clip (25) was found in the *Ruppia* habitat during July, 1978, when mean species abundances in the *Zostera* (17) and mixed (18) habitats were also relatively high (Fig. 6). Approximately ten or fewer species were present in September, 1979, epifaunal samples. *Zostera* samples contained slightly higher species numbers on three of the six sample dates (October 1978, June, November, 1979) than either *Ruppia* or mixed samples. During April and September, 1979, mean species abundances were almost equal between these habitats. No seasonal trends were evident in the species abundance data.

A logarithmic plot of the mean abundance expressed as individuals per m^2 of vegetated bottom indicates the presence of large numbers of individuals in the epifaunal community (Fig. 7). Numbers ranged from approximately 2000 per m^2 in the *Ruppia* area (November, 1979) to almost 60,000 in *Zostera* samples (June, 1979). The variation within a single sample date was sometimes almost as great (June, 1979) with no consistent patterns of individual abundances from one habitat to the next appearing in the data.

The amount of vegetation expressed as grams dry weight/m^2 varied temporally, yet patterns of relative mean individual abundances per gram of vegetation (Fig. 8) were similar to those plotted on an aerial basis alone (Fig. 7). Only the July 1978 data showed a slight variation from the latter pattern. Mean numbers of individuals varied from almost 30 per gram of grass (*Ruppia*, November 1979) to a maximum of about 7,400 per gram (*Ruppia*, April, 1979). No clear seasonal pattern was seen. Between habitat patterns were also difficult to ascertain although generally there was a decreasing trend in the number of individuals per gram of *Ruppia* than for the other two vegetated habitats.

Shannon diversity (H') calculated for epifaunal samples generally tended to be higher for the *Ruppia* area than for the mixed or *Zostera* areas (Fig. 9). Lowest diversities were seen during September and November, 1979, in all but the *Ruppia* area which experienced its lowest diversity in April, 1979. Seasonal patterns in species diversity were obscure but in general when progressing from spring through summer to fall, the diversity of the epifauna associated with both *Zostera* and mixed stands of vegetation decreased whereas diversity in the *Ruppia* zone tended to increase.

An examination of the top ten epifaunal species associated with each habitat (Tables 8-13) revealed that they were present as one of the top ten species in all habitats without regard to vegetation type. For example, the isopod *Erichsonella attenuata*, barnacle *Balanus improvisus*, gastropods

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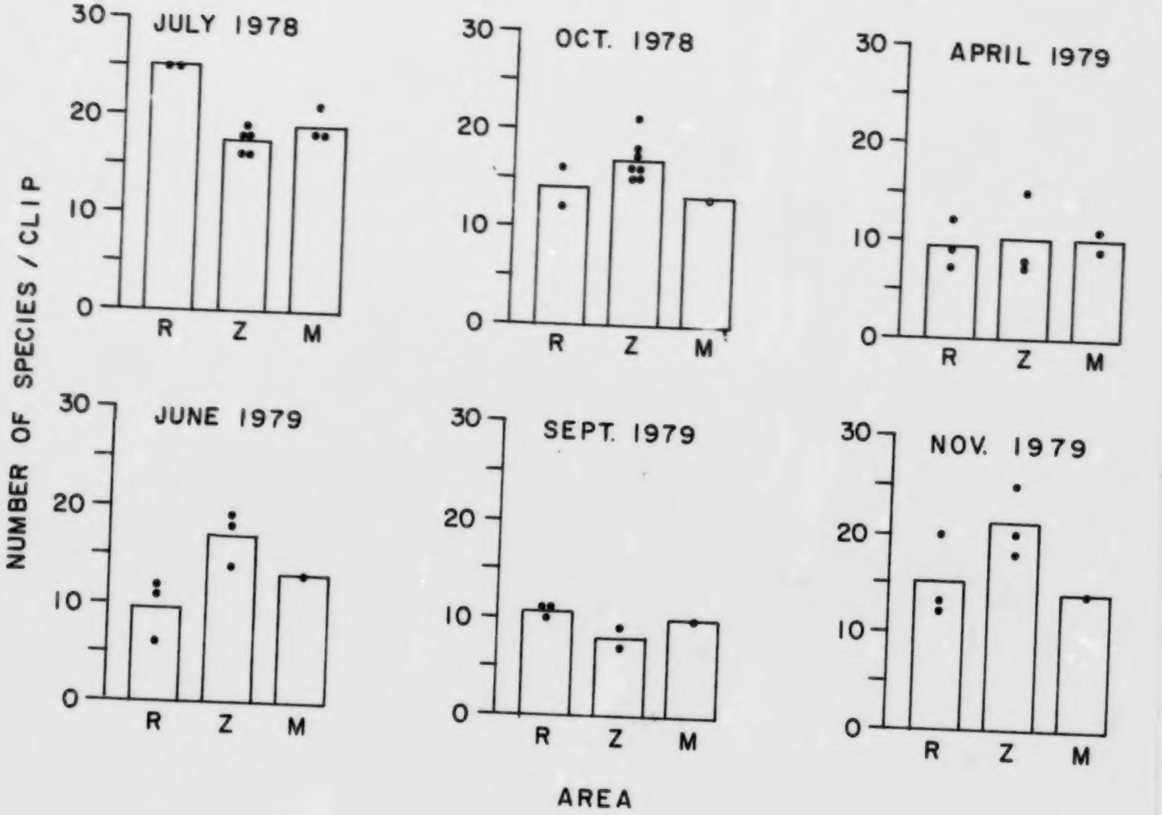

Fig. 6. Number of epifaunal species per clip (0.1 m^2) found for each vegetated zone of the grassbed. Treatment designations are as follows: R = *Ruppia maritima*; Z = *Zostera marina*; M = mixed vegetation. Closed circles indicate number of species for each clip. Boxes represent the mean number of species per clip for each area.

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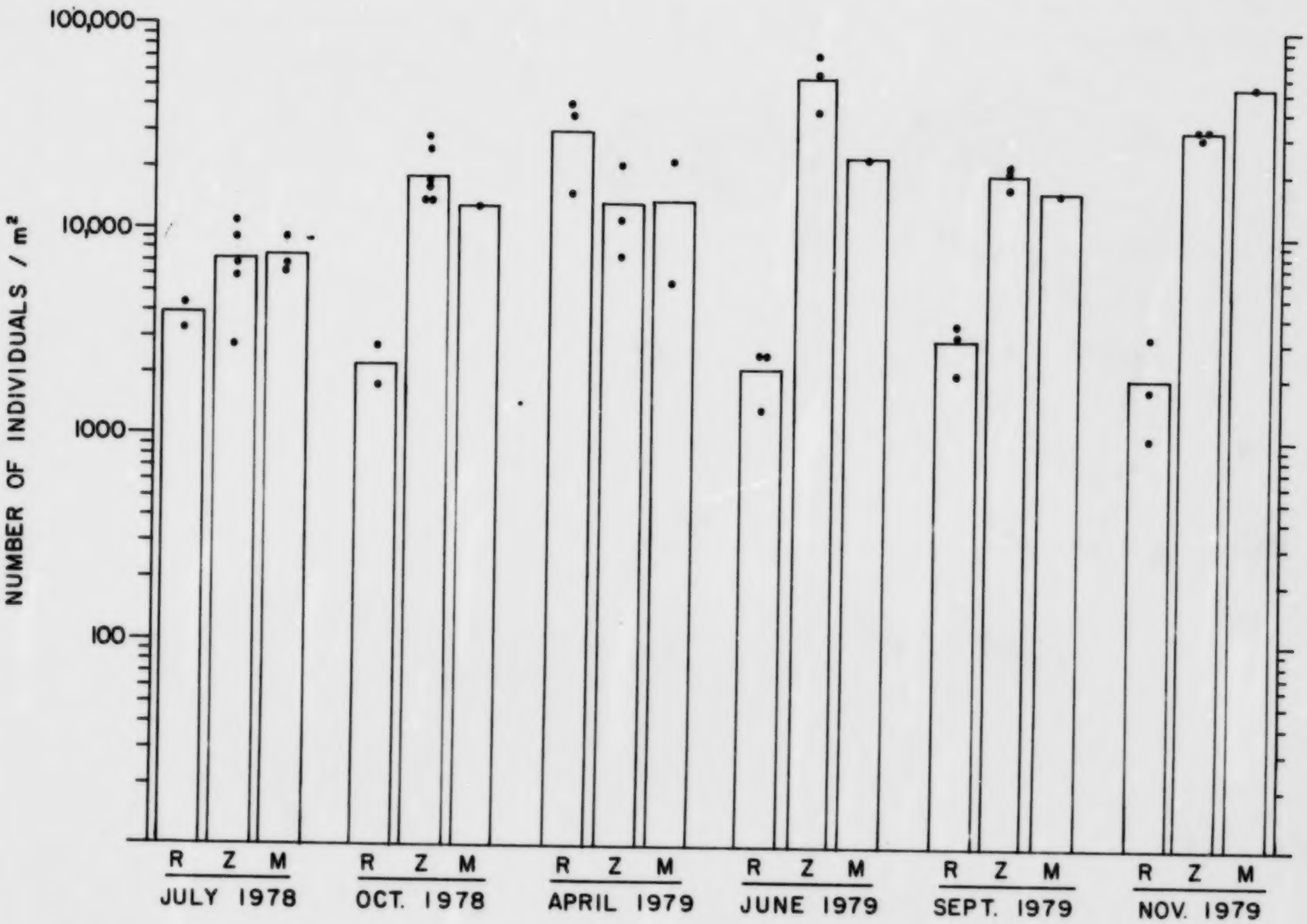

Fig. 7. Epifaunal abundance expressed as number of individuals per m^2 for each vegetated zone in the grassbed. Treatment designations are as follows: R = Ruppia maritima; Z = Zostera marina; M = mixed vegetation. Closed circles indicate number of individuals per m^2 for each sample. Boxes represent the mean number of individuals per m^2 for each area.

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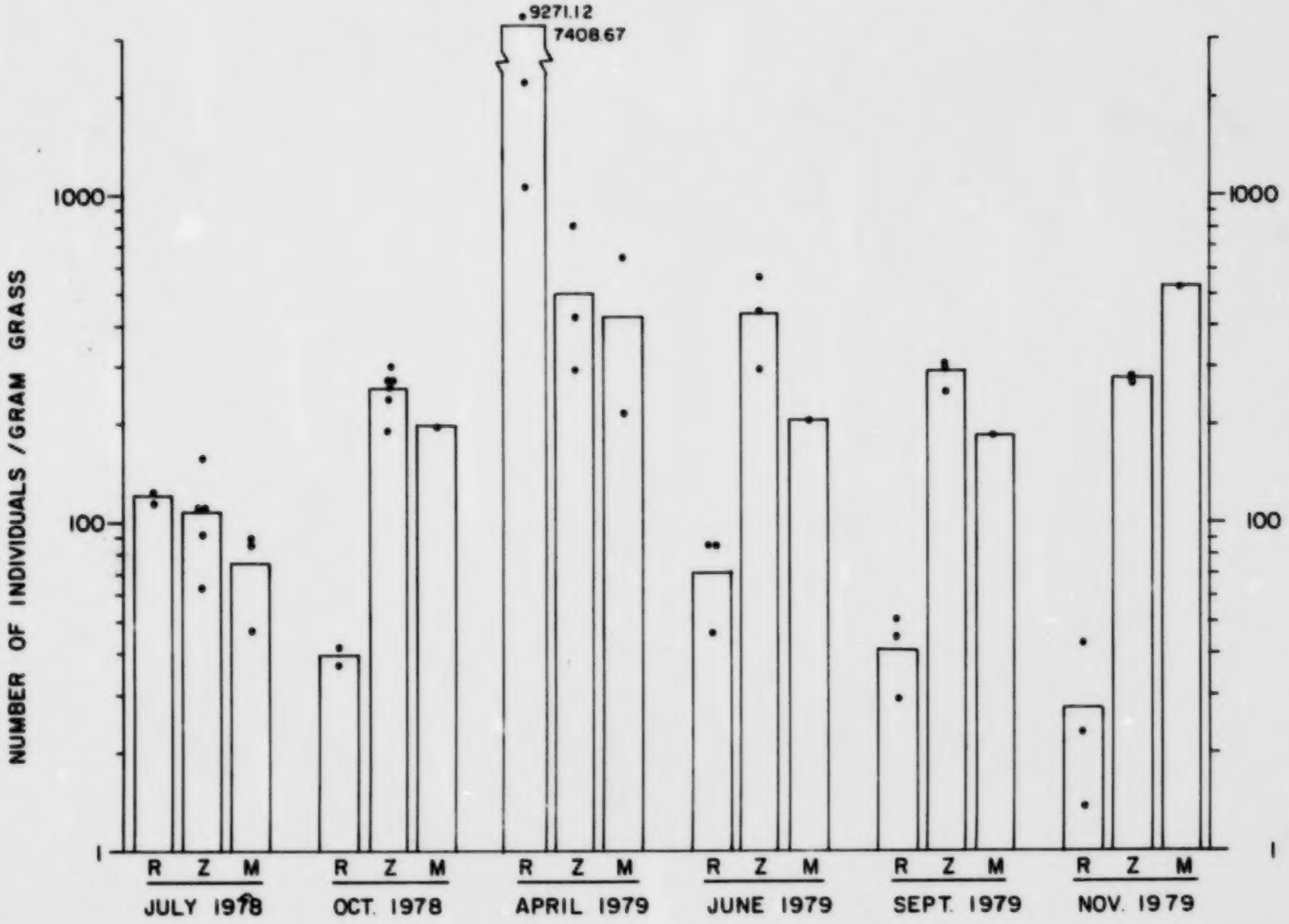

Fig. 8. Epifaunal abundance expressed as the number of individuals per gram of grass for the three vegetated zones within the grassbed. Treatment designations are as follows: R = *Ruppia maritima*; Z = *Zostera marina*; M = mixed vegetation. Closed circles indicate the number of individuals per gram of grass for each clip. Boxes represent the mean number of individuals per gram of grass for each area.

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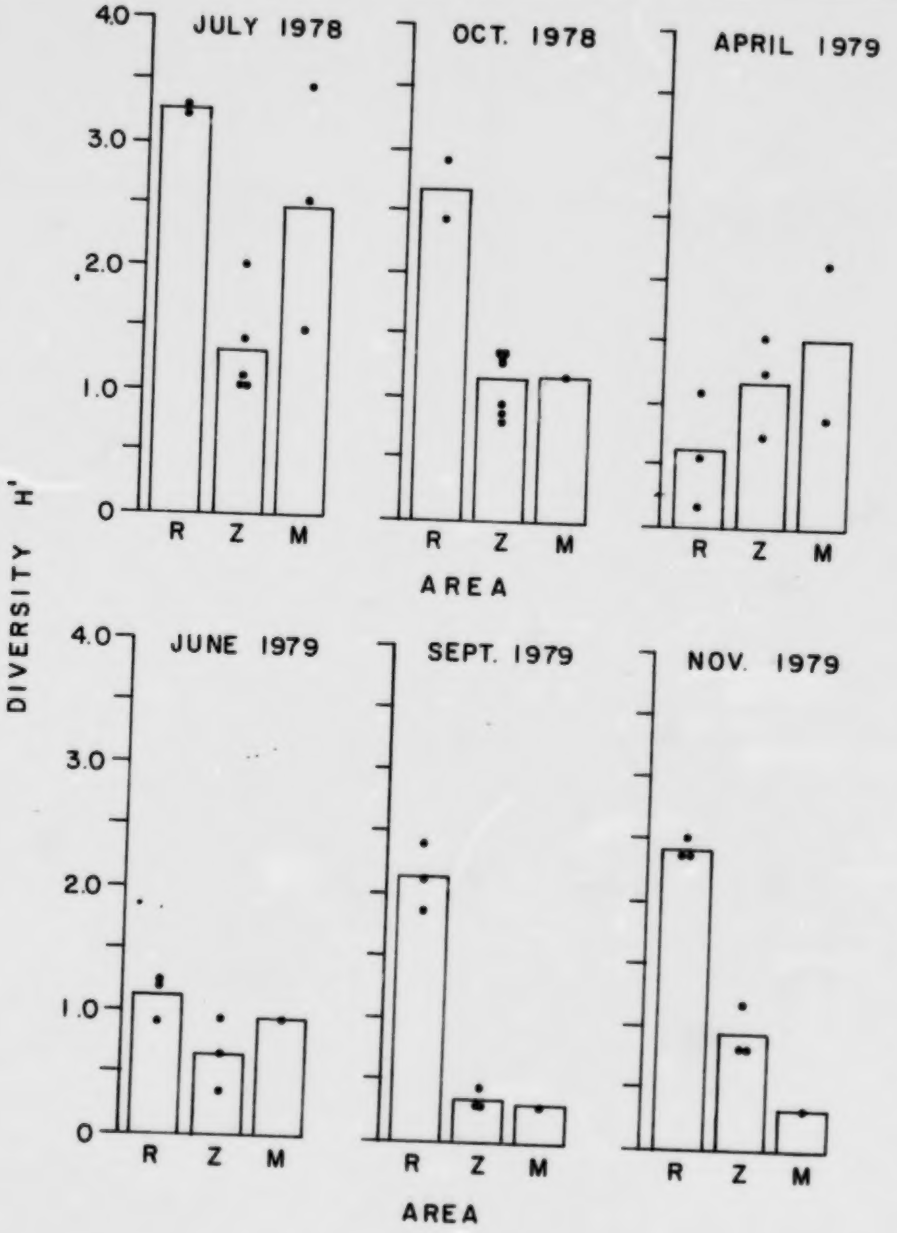

Fig. 9. Epifaunal species diversity (Shannon H') for each vegetated zone in the grassbed. Treatment designations are as follows: R = *Ruppia maritima*; Z = *Zostera marina*; M = mixed vegetation. Closed circles indicate the diversity for each core. Boxes represent the mean diversity for each area.

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TABLE 8. EPIFAUNAL SPECIES RECORDED IN THE THREE DIFFERENT TYPES OF VEGETATED AREAS (*RUPPIA*, *ZOSTERA*, MIXED) AT THE VAUCLUSE SHORES STUDY SITE, JULY, 1978.

RUPPIA

Species	°/o	#/gram	#/m^2
1. *Caprella penantis*	28.26	34.05	1106.70
2. *Erichsonella attenuata*	17.26	20.80	676.04
3. *Balanus improvisus*	10.74	12.94	420.65
4. *Idotea balthica*	8.18	9.86	320.49
5. *Bittium varium*	7.03	8.47	275.42
6. *Nereis succinea*	6.27	7.55	245.38
7. *Paracaprella tenuis*	3.58	4.31	140.22
8. *Ampithoe longimana*	3.45	4.16	135.21
9. *Cymadusa compta*	3.07	3.70	120.18
10. *Gastropoda*	1.92	2.31	75.12
Total	89.76	56.38	3515.41
Total Sample	100.00	62.81	3916.46

ZOSTERA

Species	°/o	#/gram	#/m^2
1. *Crepidula convexa*	81.19	89.95	5882.41
2. *Bittium varium*	8.03	8.90	581.86
3. *Idotea balthica*	3.11	3.44	225.17
4. *Erichsonella attenuata*	1.35	1.49	97.64
5. *Polydora ligni*	1.07	1.19	77.71
6. *Balanus improvisus*	0.88	0.98	63.77
7. *Ampithoe longimana*	0.80	0.88	57.79
8. *Paracaprella tenuis*	0.61	0.67	43.84
9. *Nereis succinea*	0.44	0.49	31.88
10. *Doridella obscura*	0.44	0.49	31.88
Total	97.92	108.89	7093.95
Total Sample	100.00	111.20	7244.64

MIXED

Species	°/o	#/gram	#/m^2
1. *Crepidula convexa*	40.77	28.87	3088.59
2. *Bittium varium*	15.68	11.10	1187.41
3. *Balanus improvisus*	10.57	7.48	800.50
4. *Caprella penantis*	6.08	4.30	460.29
5. *Erichsonella attenuata*	5.55	3.93	420.26
6. *Ampithoe longimana*	4.93	3.49	373.57
7. *Idotea balthica*	3.74	2.65	283.51
8. *Gastropoda*	2.64	1.87	200.12
9. *Polydora ligni*	2.20	1.56	166.77
10. *Nereis succinea*	2.03	1.43	153.43
Total	94.19	66.68	7134.45
Total Sample	100.00	70.79	7574.53

TABLE 9. EPIFAUNAL SPECIES RECORDED IN THE THREE DIFFERENT TYPES OF VEGETATED AREAS (*RUPPIA*, *ZOSTERA*, MIXED) AT THE VAUCLUSE SHORES STUDY SITE, OCTOBER, 1978.

RUPPIA

Species	$^{o}/_{o}$	#/gram	#/m^2
1. *Crepidula convexa*	40.58	16.37	916.64
2. *Bittium varium*	18.85	7.60	425.76
3. *Ampithoe longimana*	9.98	4.03	225.40
4. *Erichsonella attenuata*	9.09	3.67	205.37
5. *Paracaprella tenuis*	4.88	1.97	110.20
6. *Nereis succinea*	3.10	1.25	70.13
7. *Caprella penantis*	3.10	1.25	70.13
8. *Cymadusa compta*	2.66	1.07	60.11
9. *Astyris lunata*	1.77	0.72	40.07
10. *Balanus improvisus*	1.77	0.72	40.07
Total	95.78	38.65	216.88
Total sample	100.00	40.35	226.44

ZOSTERA

Species	$^{o}/_{o}$	#/gram	#/m^2
1. *Crepidula convexa*	81.89	211.65	15177.76
2. *Bittium varium*	6.79	17.56	1259.35
3. *Amphithoe longimana*	2.80	7.24	519.14
4. *Balanus improvisus*	2.08	5.37	385.08
5. *Erichsonella attenuata*	1.59	4.12	295.23
6. *Paracaprella tenuis*	1.38	3.56	255.29
7. *Astyris lunata*	1.06	2.74	196.82
8. *Caprella penantis*	0.95	2.47	176.85
9. *Anadara transversa*	0.30	0.78	55.62
10. *Nereis succinea*	0.15	0.38	27.10
Total	98.99	256.14	18348.24
Total sample	100.00	258.75	18535.45

MIXED

Species	$^{o}/_{o}$	#/gram	#/m^2
1. *Crepidula convexa*	78.85	156.30	10471.85
2. *Bittium varium*	11.58	22.96	1538.52
3. *Balanus improvisus*	3.44	6.81	456.59
4. *Erichsonella attenuata*	2.84	5.63	377.19
5. *Ampithoe longimana*	0.67	1.33	89.33
6. *Paracaprella tenuis*	0.67	1.33	89.33
7. *Nereis succinea*	0.45	0.89	59.56
8. *Astyris lunata*	0.45	0.89	59.56
9. *Cymadusa compta*	0.45	0.89	59.56
10. *Anadara transversa*	0.37	0.74	49.63
Total	99.77	197.77	13251.12
Total sample	100.00	198.23	13281.67

TABLE 10. EPIFAUNAL SPECIES RECORDED IN THE THREE DIFFERENT TYPES OF VEGETATED AREAS (*RUPPIA*, *ZOSTERA*, MIXED) AT THE VAUCLUSE SHORES STUDY SITE, APRIL, 1979.

RUPPIA

Species	°/o	#/gram	$\#/m^2$
1. *Polydora ligni*	93.55	6103.23	30516.13
2. *Crepidula convexa*	1.42	92.90	464.52
3. *Bittium varium*	1.32	85.16	425.81
4. *Caprella penantis*	1.11	72.26	361.29
5. *Paracaprella tenuis*	0.75	49.03	245.16
6. *Gammarus mucronatus*	0.71	46.45	232.26
7. *Erichsonella attenuata*	0.63	41.29	206.45
8. *Balanus improvisus*	0.16	10.32	51.61
9. *Astyris lunata*	0.12	7.74	38.71
10. *Cymadusa compta*	0.12	7.74	38.71
Total	99.89	6516.12	32580.65
Total sample	100.00	6523.30	32616.53

ZOSTERA

Species	°/o	#/gram	$\#/m^2$
1. *Polydora ligni*	81.18	423.48	11433.84
2. *Crepidula convexa*	10.50	54.78	1478.98
3. *Caprella penantis*	2.91	15.20	410.28
4. *Gammarus mucronatus*	2.81	14.65	395.54
5. *Bittium varium*	1.12	5.82	157.23
6. *Paracaprella tenuis*	0.63	3.28	88.44
7. *Microprotopus raneyi*	0.31	1.64	44.22
8. *Cerapis tubularis*	0.19	1.00	27.02
9. *Nereis succinea*	0.09	0.45	12.28
10. *Astyris lunata*	0.09	0.45	12.28
Total	99.83	520.75	14050.11
Total sample	100.00	521.64	14074.04

MIXED

Species	°/o	#/gram	$\#/m^2$
1. *Polydora ligni*	80.16	371.47	11701.43
2. *Crepidula convexa*	7.93	36.77	1158.16
3. *Gammarus mucronatus*	2.74	12.68	389.37
4. *Caprella penantis*	2.19	10.14	319.49
5. *Bittium varium*	1.92	8.87	279.56
6. *Paracaprella tenuis*	1.64	7.61	239.62
7. *Astyris lunata*	0.96	4.44	139.78
8. *Microprotopus raneyi*	0.96	4.44	139.78
9. *Balanus improvisus*	0.68	3.17	99.84
10. *Erichsonella attenuata*	0.41	1.90	59.90
Total	99.59	461.49	14526.93
Total sample	100.00	463.39	14586.74

TABLE 11. EPIFAUNAL SPECIES RECORDED IN THE THREE DIFFERENT TYPES OF VEGETATED AREAS (*RUPPIA*, *ZOSTERA*, MIXED) AT THE VAUCLUSE SHORES STUDY SITE, JUNE, 1979.

RUPPIA

Species	$^{o}/_{o}$	#/gram	#/m^2
1. *Balanus improvisus*	79.83	55.44	1663.12
2. *Polydora ligni*	8.51	59.1	177.30
3. *Caprella penantis*	4.34	3.01	90.43
4. *Erichsonella attenuata*	4.09	2.84	85.11
5. *Nereis succinea*	1.19	0.83	24.82
6. *Stylochus ellipticus*	0.51	0.35	10.64
7. *Bittium varium*	0.34	0.24	7.09
8. *Cymadusa compta*	0.26	0.18	5.32
9. *Astyris lunata*	0.17	0.12	3.55
10. *Paracaprella tenuis*	0.17	0.12	3.55
Total	98.41	69.04	2070.93
Total sample	100.00	70.16	2104.39

ZOSTERA

Species	$^{o}/_{o}$	#/gram	#/m^2
1. *Balanus improvisus*	91.28	397.80	52907.24
2. *Polydora ligni*	2.68	11.67	1552.71
3. *Gammarus mucronatus*	1.62	7.08	941.04
4. *Stylochus ellipticus*	1.24	5.39	716.23
5. *Crepidula convexa*	1.11	4.83	643.04
6. *Nereis succinea*	0.68	2.95	392.10
7. *Erichsonella attenuata*	0.21	0.90	120.24
8. *Bittium varium*	0.19	0.83	109.79
9. *Caprella penantis*	0.19	0.83	109.79
10. *Astyris lunata*	0.16	0.71	94.10
Total	99.36	432.99	57586.26
Total sample	100.00	435.78	57957.19

MIXED

Species	$^{o}/_{o}$	#/gram	#/m^2
1. *Balanus improvisus*	86.61	180.05	20165.20
2. *Crepidula convexa*	4.69	9.74	1091.42
3. *Gammarus mucronatus*	2.23	4.64	591.72
4. *Erichsonella attenuata*	2.01	4.18	467.75
5. *Polydora ligni*	1.79	3.71	415.78
6. *Stylochus ellipticus*	0.78	1.62	181.90
7. *Nereis succinea*	0.45	0.93	103.94
8. *Astyris lunata*	0.45	0.93	103.94
9. *Ampithoe longimana*	0.33	0.70	77.96
10. *Nassarius obsoletus*	0.33	0.70	77.96
Total	99.67	207.20	23205.57
Total sample	100.00	207.89	23282.40

TABLE 12. EPIFAUNAL SPECIES RECORDED IN THE THREE DIFFERENT TYPES OF VEGETATED AREAS (RUPPIA, ZOSTERA, MIXED) AT THE VAUCLUSE SHORES STUDY SITE, SEPTEMBER, 1979.

RUPPIA

Species	°/o	#/gram	#/m^2
1. Erichsonella attenuata	55.84	23.15	1620.46
2. Balanus improvisus	16.23	6.73	471.06
3. Crepidula convexa	9.09	3.77	263.80
4. Cymadusa compta	3.90	1.62	113.06
5. Gastropoda	3.57	1.48	103.63
6. Mollusca	3.57	1.48	103.63
7. Nereis succinea	3.25	1.35	94.21
8. Bittium varium	1.95	0.81	56.53
9. Paracaprella tenuis	0.65	0.27	18.84
10. Stylochus ellipticus	0.32	0.13	9.42
Total	98.37	40.79	2854.64
Total sample	100.00	41.47	2901.94

ZOSTERA

Species	°/o	#/gram	#/m^2
1. Crepidula convexa	96.02	278.90	18685.96
2. Gastropoda	1.24	3.59	240.61
3. Balanus improvisus	0.97	2.82	188.78
4. Erichsonella attenuata	0.57	1.66	111.05
5. Idotea balthica	0.27	0.77	51.82
6. Bittium varium	0.19	0.55	37.02
7. Doridella obscura	0.17	0.50	33.31
8. Stylochus ellipticus	0.13	0.39	25.91
9. Astyris lunata	0.10	0.28	18.51
10. Ampithoe longimana	0.08	0.22	14.81
Total	99.74	289.68	19407.78
Total sample	100.00	290.44	19458.37

MIXED

Species	°/o	#/gram	#/m^2
1. Crepidula convexa	96.74	180.32	15868.56
2. Erichsonella attenuata	0.82	1.52	133.87
3. Balanus improvisus	0.54	1.01	89.25
4. Gastropoda	0.49	0.91	80.32
5. Nereis succinea	0.38	0.71	62.47
6. Idotea balthica	0.38	0.71	62.47
7. Paracaprella tenuis	0.33	0.61	53.55
8. Bittium varium	0.16	0.30	26.77
9. Ampithoe longimana	0.11	0.20	17.85
10. Anadara transversa	0.05	0.10	8.92
Total	100.00	186.39	16404.03
Total sample	100.00	186.39	16404.03

TABLE 13. EPIFAUNAL SPECIES RECORDED IN THE THREE DIFFERENT TYPES OF VEGETATED AREAS (*RUPPIA*, *ZOSTERA*, MIXED) AT THE VAUCLUSE SHORES STUDY SITE, NOVEMBER, 1979.

RUPPIA

Species	$^o/_o$	#/gram	#/m^2
1. *Erichsonella attenuata*	38.11	9.26	675.84
2. *Crepidula convexa*	28.11	6.83	498.49
3. *Cymadusa compta*	7.84	1.90	139.00
4. *Paracaprella tenuis*	5.14	1.25	91.07
5. *Nereis succinea*	4.59	1.12	81.48
6. *Gastropoda*	1.89	0.46	33.55
7. *Balanus improvisus*	1.89	0.46	33.55
8. *Oxyurostylis smithi*	1.89	0.46	33.55
9. *Gammarus mucronatus*	1.35	0.33	23.97
10. *Caprella penantis*	1.35	0.33	23.97
Total	92.16	22.40	1634.47
Total sample	100.00	24.31	1773.51

ZOSTERA

Species	$^o/_o$	#/gram	#/m^2
1. *Crepidula convexa*	88.19	243.60	28013.67
2. *Balanus improvisus*	2.66	7.34	844.34
3. *Idotea balthica*	2.56	7.06	811.61
4. *Doridella obscura*	1.09	3.02	346.90
5. *Ampithoe longimana*	1.07	2.96	340.35
6. *Erichsonella attenuata*	0.95	2.62	301.08
7. *Polydora ligni*	0.58	1.59	183.27
8. *Caprella penantis*	0.54	1.48	170.18
9. *Gastropoda*	0.45	1.25	144.00
10. *Gammarus mucronatus*	0.29	0.80	91.63
Total	98.38	271.72	31250.03
Total sample	100.00	276.19	31764.62

MIXED

Species	$^o/_o$	#/gram	#/m^2
1. *Crepidula convexa*	96.13	506.42	51401.82
2. *Erichsonella attenuata*	1.74	9.17	931.19
3. *Balanus improvisus*	1.18	6.19	628.55
4. *Polydora ligni*	0.26	1.38	139.68
5. *Gastropoda*	0.20	1.03	104.76
6. *Doridella obscura*	0.17	0.92	93.12
7. *Idotea balthica*	0.13	0.69	69.84
8. *Nereis succinea*	0.04	0.23	23.28
9. *Bittium varium*	0.04	0.23	23.28
10. *Stylochus ellipticus*	0.02	0.11	11.64
Total	99.91	526.37	53427.16
Total sample	100.00	526.84	53475.29

Crepidula convexa and Bittium varium and the polychaete Nereis succinea were all commonly ranked among the top ten species in all vegetated habitats. Seasonal pulses of abundance for B. improvisus (June, 1979) and Polydora ligni (April, 1979) were evident in the data with possibly similar evidence for Crepidula convexa and Bittium varium.

The results presented here indicate that the grassbed and each of the sandy habitats are distinct with respect to their associated fauna. Differences between the vegetated habitats are less clear cut. The number of species and individuals was greatly increased in the vegetated habitats indicating their importance to the Chesapeake Bay fauna.

DISCUSSION

A primary understanding of the structural aspects of vegetated habitats is necessary to further examine the functional roles of the organisms within these habitats. Additionally, a comparison of grass bed community structure with that of nonvegetated areas can provide greater insight into the importance of the various habitats surveyed.

We have clearly demonstrated an increased abundance of infauna, particularly oligochaetes, at depths of 6 to 15 cm below the sediment surface in vegetated areas compared to exposed sandy bottoms. Infauna living in grass beds apparently derive some advantage from the root and rhizome system of the plants. The redox potential discontinuity layer (RPD) in grass beds is farther below the sediment surface than in unvegetated habitats and probably allows organisms to survive deeper in the sediments. Oxygenation of surficial sediment by the rhizosphere increases the two dimensionality of the habitat in which grass bed associated infauna live. Virtually no information exists on the rhizofauna of marine grasses although related studies in salt marshes have demonstrated the rhizosphere to be important in determining the vertical distribution of associated infauna (Bell et al. 1978; Teal and Wieser, 1966).

Additional advantages provided by vegetation to the infaunal community include increased sediment stability and protection from predation. Seagrasses have been shown to stabilize sediments by their current baffling and wave damping action (Hartog, 1970; Taylor and Lewis, 1970; Zieman, 1972). Orth (1977) experimentally demonstrated that such sediment stability caused increased infaunal diversity and density. In addition, observations made on blue crab feeding prompted Orth (1977) to suggest that such activities were hampered by the presence of the root and rhizome layer in Zostera beds. A similar hypothesis suggesting the protection provided by the rhizosphere to the infauna was made by Riese (1977). All three factors acting together (increased oxygenation of the sediments, greater sediment stability and protection from predation) probably account for the high infaunal densities and species abundances observed in our study.

Besides the functional advantages provided by the root and rhizome system of aquatic vegetation, decomposing leaf litter supplies a rich detrital food source for the grass bed infauna (Thayer, et al. 1977; Fenchell, 1972). For species living among the plants, this food source is readily accessible and probably enhances the structural magnitude and diversity of the grass bed infaunal community to the degree observed in our study.

The only exception to increased individual abundances in the grass bed infauna occurred during the July, 1978 sample date when the inside sand habitat showed the greatest abundance of individuals. This high level was caused by a *Gemma gemma* recruitment pulse bringing the total number of individuals to just over 33,000 per meter squared. Similar increases in the small gastropod *Odostomia* spp. were also observed. This species is parasitic on *Gemma gemma* (Abbott, 1974) and showed a positive response to an increased food source.

Population dynamics of species comprising the infaunal community are evident in our data and emphasize the continually changing nature of the dominance hierarchy over time. Also evident is persistence of certain abundant species in the habitats studied imparting some degree of constancy to the community associated with each habitat. The amphipod *Acanthohaustoris millsi* and polychaete *Paraonis fulgens* were numerous and almost exclusively found in the dynamic offshore sand bar (OS) habitat. Both were always present as one of the top ten in this habitat for the duration of our study. *Acanthohaustorius millsi*, a burrowing amphipod, is a suspension feeder on microscopic algae and detritus and is commonly found at the low tide mark as well as subtidally on sandy beaches (Dexter, 1969). It is associated with dynamic medium sands such as those of the sand bar area. Similarly, *Paraonis fulgens*, described as both a non-selective burrowing deposit feeder and a highly selective diatom grazer (Fauchald and Jumars, 1979) was also found in all OS samples. It constituted the most abundant species at all sample times except during July 1978 when it was third in abundance. These species are both adapted for living in shifting sediments and are apparently unable to compete successfully in the more stable protected sandy bottom within the grass bed.

The small bivalve, *Gemma gemma*, is able to exist in both the more turbulent offshore sandbar habitat and the sandy patches within the grass bed. Species which more accurately distinguish the bare sand zones inside the vegetated area include the opportunistic capitellid polychaete, *Capitella capitata*, as well as the spionid polychaete, *Scolelepis squamatus*. Surprisingly, neither of these species was among the ten most numerous ones in grass bed infaunal samples although the latter species was occasionally found on the offshore sandbar. *Capitella capitata* builds tubes at or near the sediment surface and *Scolelepis squamatus* builds loosely constructed burrows in sandy substrates (Fauchald and Jumars, 1979). *Capitella capitata* is known to be an r- strategist (high fecundity and short life span) and, based on our data is recruited in the late summer and early fall. *Scolelepis squamatus* persisted throughout the study in the inside sand habitat.

The grass bed infaunal community contained a more varied group overall of species comprising the top ten during the course of our study than that exhibited for either of the sandy habitats. This fact reflects the diverse and dynamic nature of the community with a variety of species recruiting and subsequently decreasing in abundance through time. Those species which occurred most abundantly and regularly included the polychaete *Heteromastus* *filiformis*, *Polydora ligni*, *Nereis succinea* and numerous unidentified oligochaetes. *Heteromastus filiformis* is a deep burrowing opportunistic capitellid that was abundant in the grass bed proper and in sand patches within the vegetated zone as were unidentified oligochaetes. Both *P. ligni* (Spionidae) and *N. succinea* (Nereidae) were numerous in the grass bed but were rarely encountered in the two sandy habitats. The former species has been described as the most abundant species in estuarine waters of the Chesapeake Bay (Wass, 1965) with peak abundances on *Zostera marina* occurring in April and May (Marsh, 1970). Orth (1971) found peaks in larval abundance in the York River to occur in April. Despite its distinct seasonal pulses, *P. ligni* was the most abundant polychaete throughout the year on fouling panels in Hampton Roads, Virginia (Calder, 1966). In our study, *P. ligni* persisted as one of the top ten species in all three types of vegetated areas during the entire study. *Nereis succinea* likewise was constantly abundant. This highly opportunistic species has been described as a surface deposit feeder as well as an omnivore feeding on prey (i.e. other *Nereis*) and silt-clay to sand sized particles and plant detritus (Dauer, 1980). Not only was *N. succinea* commonly found infaunally, it also was an abundant epifaunal community member.

The isopods *Edotea triloba* and *Erichsonella attenuata* were also numerous and routinely present in infaunal samples. *Edotea* is epibenthic and was rarely found in the epifauna whereas *Erichsonella* was common in both communities.

The infaunal community of eelgrass beds at Vaucluse Shores was similar to those of Guinea Marsh grassbeds studied by Orth (1973). Polychaetes (*Heteromastus filiformis*, *Streblospio benedicti*, *Nereis succinea*, *Polydora ligni* and to a lesser extent *Spiochaetopterus oculatus* and *Scoloplos robustus*) were among the most numerous species present in both studies. Oligochaetes and the isopod *Edotea triloba* were similarly abundant. It appears that an infaunal community occurs within grassbeds which distinguishes those areas from non-vegetated sand bottoms and furthermore characterizes them in terms of general dominance hierarchies and species abundances.

The epifaunal community was comprised of numerous species all of which utilized the grass blades as a substrate and a feeding area. The barnacle, *Balanus improvisus*, gastropods, *Bittium varium* and *Crepidula convexa*, isopod, *Erichsonella attenuata* and amphipod, *Caprella penantis* were all abundant in grassbed epifaunal samples. They occurred consistently among the top ten species in all vegetated habitats without regard to vegetation type. Some species such as *Bittium varium* and *Crepidula convexa* were more abundant on *Zostera marina*. Their prevalence on eelgrass is probably related to the morphology of the plant, with the wide bladed species preferred to those such as *Ruppia maritima* with narrow blades. *Bittium varium* feeds extensively on eelgrass periphyton (see grazing section, this report) and its great abundance in the epifauna is probably related to the readily available food supply. Although juvenile *Crepidula convexa* are thought to be microalgal grazers as well, adults switch to a filter feeding mode (Hoagland, 1975) and therefore use grassblades primarily as an attachment platform from which to feed. *Caprella penantis* is the most common caprellid amphipod along the east coast of the United States and occurs abundantly from Long Island to the Chesapeake Bay. It is nonspecific in its habitat preference, occurring on a wide variety of substrates including algae, sponges, alcyonarians and particularly hydroids (McCain, 1968). *Erichsonella attenuata*, an isopod, is characteristically associated with eelgrass (Schultz, 1969) although in our study it was also common on *Ruppia maritima*. Little is known about the biology of this species. It is probably omnivorous and occurs in such great abundance in grassbeds because of the large quantities of suitable food and habitat.

Not surprisingly, several of the dominant species found in the Vaucluse Shores epifauna were also present in a York River epifaunal community studied by Marsh (1973, 1976). Of the 5 most abundant species found by Marsh (1973), four (*Bittium varium*, *Crepidula convexa*, *Erichsonella attenuata* and *Ampithoe longimana*) were also dominants at Vaucluse Shores. *Paracerceis caudata* an epifaunal isopod was commonly found in the Chesapeake Bay during the time of Marsh's study in 1967 and 1968 but declined drastically in abundance after the devastating passage of hurricane Agnes in June of 1972 (Orth, 1976). Their populations do not yet seem to have recovered which accounts for the absence of *P. caudata* during our study. Some species which were abundant for brief periods during the year in Marsh's (1975) study were regularly abundant in the Vaucluse Shores epifauna. These include the barnacle, *Balanus improvisus* and epifaunal polychaete, *Polydora ligni*. Both the ascidian, *Molgula manhattensis* and saccoglossan, *Ercolania fuscata* were periodically abundant in the York River but were uncommon in Vaucluse Shores samples. Reasons for this fact are unclear.

We have demonstrated and confirmed the existence of a diverse and abundant infaunal and epifaunal community associated with a vegetated habitat in the lower Chesapeake Bay. Marine grasses create greater physical complexity resulting in a more heterogeneous habitat that is capable of supporting larger numbers of invertebrate species and individuals than adjacent sandy areas. Fish are attracted to these meadows because of the preponderence of invertebrates which are heavily preyed upon (Adams, 1976a, b,c; Nelson, 1979; Young and Young 1978; Stoner, 1979; Orth and Heck, 1980). Many of the fish (e.g. spot and speckled trout) which frequent grassbeds are commercially harvested or are important recreational species. Grassbeds are also an important refuge for both juvenile as well as older blue crabs, *Callinectes sapidus*, during the soft shell phase of their molt cycle. Thus the demise of these habitats may have serious consequences to many species although the effects of such declines may take years to be felt.

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CHAPTER 2

PREDATOR EXCLUSION EXPERIMENTS IN A CHESAPEAKE BAY GRASS COMMUNITY

by

Robert J. Orth

and

Jacques van Montfrans

ABSTRACT

The effects of predators on the density of eelgrass epifauna and infauna and sand infauna was studied using predator exclusion techniques. A large topless pen (20 m^2) and smaller cages (0.25 m^2) within the pen as well as outside the pen were set up in a bare sand and an adjacent grass habitat to test the hypothesis that predation has a significant effect on the structure of associated faunal communities.

The grass habitat consistently had more infaunal species per core than the sand habitat for all treatments. There were no distinct differences among the grass treatments for species infaunal numbers but in the sand, species numbers were higher in pen and cage treatments compared with the control. Except for the sand cage treatments, there was no difference between the pen and cage treatments for number of species in both habitats.

Density of individuals in the grass habitat treatments was generally higher than the sand habitat treatments except for the June cage treatments. In the sand area, infaunal densities were always higher in the cage and pen treatments compared to the control while in the grass habitat only the September cage and pen treatments were higher than the control.

Epifaunal densities in the grass habitat were generally higher in cage and pen treatments than the control. Species response to these treatments were variable and controlled by the abundance of grass in the treatment.

The results of this work support recent evidence for the importance of predation for the structuring of benthic communities both in vegetated and non-vegetated habitats.

INTRODUCTION

The structure and organization of any biological community is determined by a number of internal and external factors, both abiotic and biotic. Most abiotic factors are usually external and cannot be controlled by the community. Log damage in intertidal regions (Dayton, 1971), wave stress and storm swells (Annala, 1974; Grigg and Maragos, 1974), anchor ice (Dayton, et al. 1969, 1970) fire (Odum, 1971) and pollution stress (Wihlm, 1967; Wihlm and Dorris, 1966, 1968) have all been shown to alter the structure of the affected community.

Predation and competition are the two most often cited biological factors that control not only the structure but the function of the community. Competition for a resource, e.g. space or food, can either be through interference or exploitative competition (Peterson, 1980) while predation can be size selective (Brooks and Dodson, 1965), species selective (Dayton, 1971; Patrick, 1970) or non-selective with respect to species or size of prey.

Predation in marine soft bottom benthic communities have recently been shown to have dramatic effects on the density and diversity of the infauna (Virnstein, 1977) and has been an implied factor for structuring benthic communities associated with seagrass beds (Nelson, 1979; Heck and Orth, 1980a; Orth and Heck, 1980; Reise, 1978). Most of the above studies have relied on manipulative tools, e.g. cages, to examine the effects of predators. Though manipulative techniques have provided ecologists with some detailed insights into community dynamics, they are not without their problems, e.g. separation of cage effects from predator effects (Virnstein, 1978, 1980).

Eelgrass beds in the Chesapeake Bay have an associated infaunal and epifaunal community that has a significantly higher density and diversity than adjacent, unvegetated communities (Orth, 1975, 1977; see also Section 1 of this report). It is this dense assemblage of invertebrates that undoubtedly serve as a food source for not only invertebrate predators (e.g. blue crabs) but also vertebrate predators (e.g. fish and waterfowl). The density of some of these predators in these vegetated areas is sometimes extremely high (Orth and Heck, 1980) suggesting that their impact on epifaunal and infaunal density may be important in reducing their density.

As part of the EPA Chesapeake Bay Program's Functional Ecology of Eelgrass Study in the Lower Chesapeake Bay, the objective of this study was to determine what impact predation, excluding waterfowl, has on the overall density and diversity of both epifauna and infauna.

STUDY SITE, MATERIALS AND METHODS

All studies involving the predator exclusion experiments were conducted in a large bed of submerged grasses located in the Chesapeake Bay off Church Neck on the Delmarva Peninsula, Virginia (Fig. 1). This is the site of the intensive functional ecology of eelgrass program being used by VIMS scientists in conjunction with the Chesapeake Bay Program, Submerged Aquatic Vegetation sub-program. This site has been referred to as the Vaucluse Shores site and is situated approximately 37°25'N latitude, 76°51'W longitude.

This site is characterized by five distinct habitat types: 1) a large unvegetated intertidal sand flat adjacent to the shoreline; 2) a *Ruppia maritima* dominated community ranging in depth from mean low water (MLW) to approximately 0.3 m below MLW; 3) a mixed bed of *R. maritima* and *Z. marina* located from 0.3 to 0.6 m below MLW; 4) a *Z. marina* dominated community located from 0.6 to 1.5 m below MLW; and 5) a second intertidal sandbar separating the grass bed from the main Chesapeake Bay.

Sampling transects were set up during an initial intensive mapping of SAV (Orth et al., 1979). Our experiments were conducted along Transect C.

In order to assess the effects of predation on the epifauna and infauna, we used two different types of exclosures. One exclosure consisted of a large circular topless pen, 5 m in diameter (20 m^2 in area). The other exclosure was a smaller, square completely enclosed cage (0.25 m^2 in area).

Two pens were constructed, one in the mixed *Ruppia-Zostera* bed and another in the adjacent inshore sandy area (Fig. 1). The pens were made of 4.3 m long salt treated wooden pilings placed 1.5 m into the bottom. Initially, thick-wall galvanized pipes (240 cm x 2 cm) were placed between the equally spaced wooden pilings to provide shape (Fig. 2). The pipes inadequately supported the weight of the netting that was placed around the pipes and were later replaced with 10 cm x 10 cm x 360 cm wooden posts. Pens were encircled by a piece of black plastic 0.63 cm mesh netting with a uv retardant (Conwed Corp Plastic Netting #OV3010). The netting, which was 324 cm wide, was attached to the posts at a height of 240 cm above the bottom. Thus, the top of the pen were always above the water. Excess netting was stapled along the bottom with 18 cm long wire staples to form an 84 cm wide skirt which extended outward from each pen. The skirt prevented predators from burrowing and gaining access into the pen. An entrance into each pen was constructed by sewing a 5 cm wide x 324 cm long strip of VELCRO to one end of the netting with the opposing piece attached to a piling.

Smaller square cages measuring 50 cm on a side and 50 cm high were constructed of reinforcing rod frames covered with the same plastic netting as used on the pens. Each cage had 30 cm long legs

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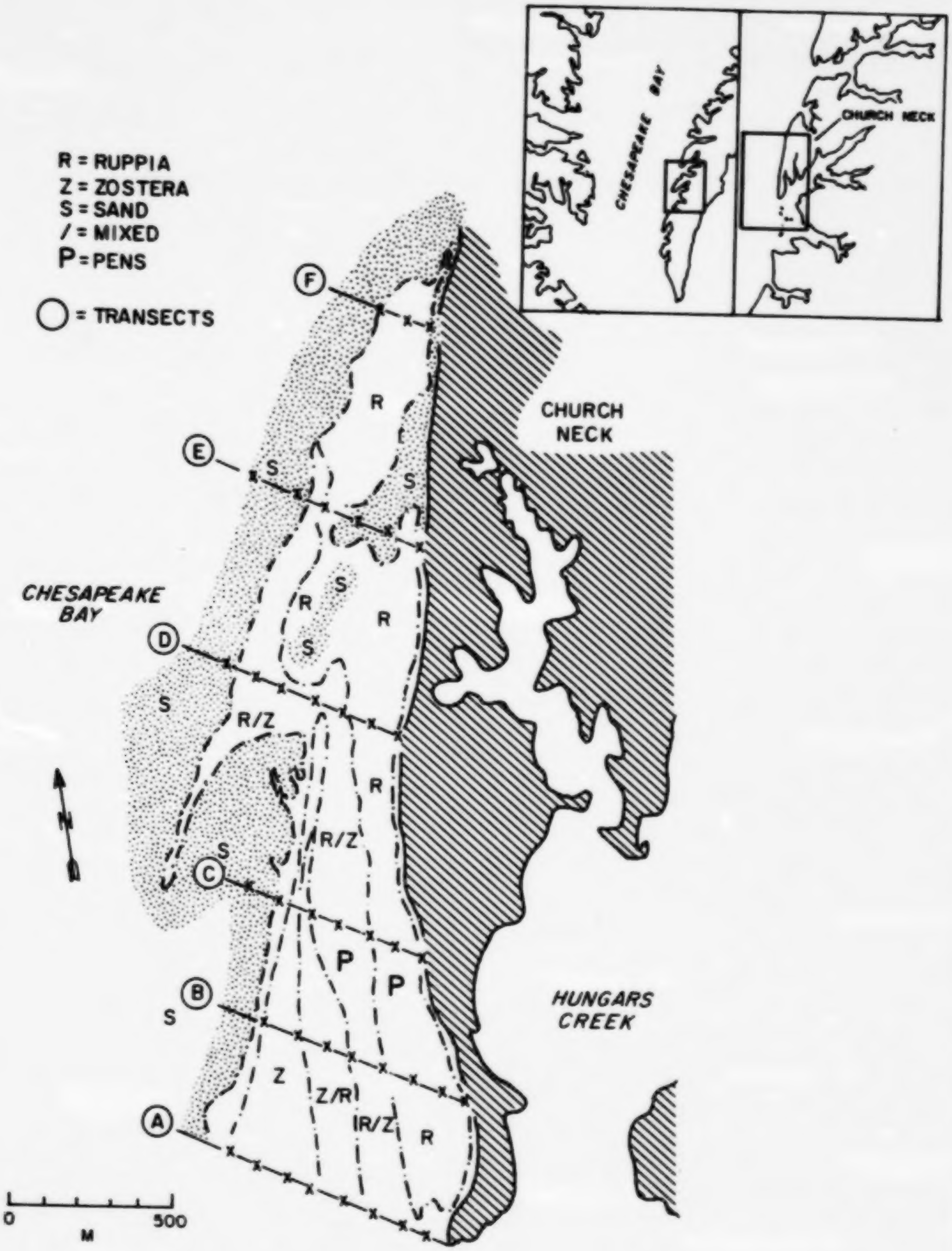
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Fig. 1. Location of study site for predator exclusion experiments.

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which were pushed into the bottom anchoring the cage. A top attached with VELCRO strips on three sides allowed easy access into each cage. Panels simulating only the sides of cages were similarly constructed to simulate some of the cage effects but still allow predator access.

The use of a large topless pen and smaller cage in combination was chosen for several reasons. Traditional caging experiments in both soft and hard substrates have relied on small cages (less than 1 m^2) with different size meshes. Cage effects such as current reduction and sediment deposition are usually associated with the use of a cage, and similarly would affect larval recruitment (Virnstein, 1978, 1980). The use of appropriate controls such as two-sided cages, and topless cages have avoided some of these problems. However, for motile predators, these controls are still not appropriate. We felt that by building a large enough pen with no top, cage effects would be considerably reduced from that of the smaller cage. The comparison between the cages and cage controls inside and outside the pen would allow us to further distinguish some of the complex cage effects.

Triads of experimental treatments were randomly arranged in triplicate both within and outside of the pens in each of the two habitats. A triad consisted of three experimental treatments: a complete cage enclosing 0.25 m^2 of bottom area, and open cage with no top and paralle sides of 0.25 m^2, and an uncaged control area (Fig. 2). One of the three triads per experimental condition (sand; sand plus pen; grass, grass plus pen) was designed to be destructively sampled after an appropriate time interval.

Pens were constructed in each of the two areas (grass and sand) in late April, 1979. Prior to setting out the cages, infauna and epifauna were sampled inside and outside the pen in both the sand and grass (see below for sampling methodologies). After the faunal sampling, the cages were placed randomly in the pen along each experimental triad as discussed above. One of each of the three triads were destructively sampled in June 12-14, September 11-13 and November 13-16, 1979.

Two days prior to the first sampling period, a strong Northeast storm destroyed the netting on the pens. Sampling for fauna was conducted according to our design after which the pens were rebuilt. In addition to the smaller mesh, a backing of heavier, large mesh (13 mm) netting (Conwed Corp. Plastic Netting #OV1580) was added for support.

Problems were also encountered with the cages in the sand area. Despite the bottom edges of the cages being placed approximately 5 cm below the sediment surface, large blue crabs burrowed under the edges and had gained entrance to these cages. Because of this disturbance, all sand cages were removed and replaced by new ones and positioned over a portion of the bottom that had been uncaged. A 24 cm wide skirt was also placed around each sand area cage. Cages in the grass area were not disturbed by crabs. These cages were left in place to

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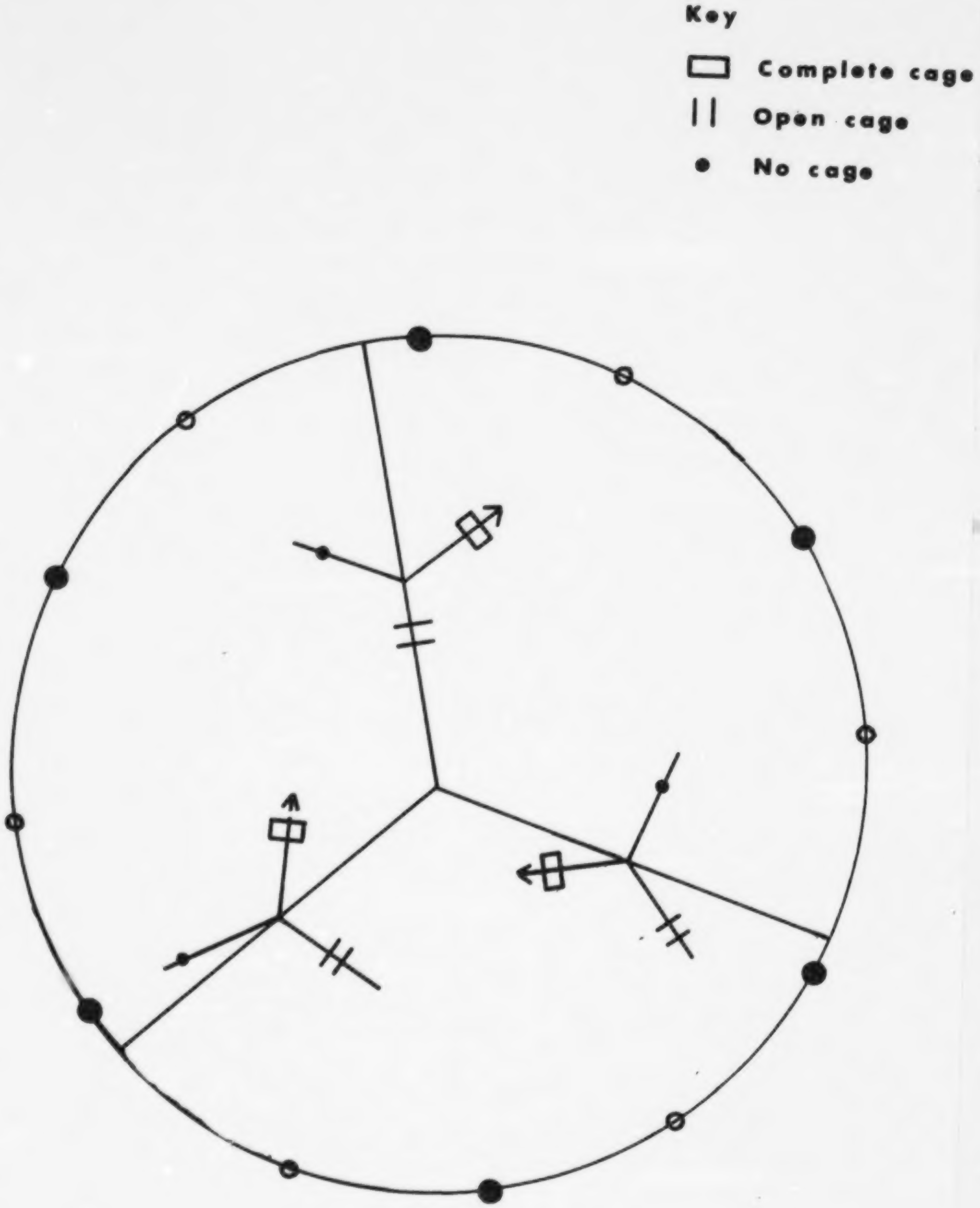

Fig. 2. Design of predator exclusion experiments showing the construction of the large pen and the placement of experimental triads. One triad consists of a complete cage, an open cage, and an area with no cage; there are three triads per large pen.

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follow the development of the community over time. In addition, new cages were placed in the grass area to parallel those that were placed in the sand area.

During each sampling period, both epifauna and infauna were sampled similarly. Samples collected within the pen were done as carefully as possible to minimize the disturbance to adjacent vegetation. Prior to the sampling, one triad was randomly designated to be sampled. Epifauna were collected first, by clipping the shoots as close as possible to the sediment surface and gently placing these blades into a collecting bag with 0.5 mm mesh bottom. If the epifaunal sample was to be taken from a caged area, the cage was first removed before sampling. All samples were taken from an area of approximately 0.1 m^2. After epifaunal samples were taken, additional grass was clipped and removed to allow for adequate space to take the infaunal samples.

After collection, epifaunal samples were kept in water and processed live by stripping all epifauna from the blades and preserving them in 10% buffered seawater with formalin containing the vital stain Rose Bengal. The remaining plant material was sorted according to species (Ruppia, Zostera, algae), oven dried at 80 C for at least 48 hours and then weighed to the nearest 0.1 g.

Infaunal samples were collected at the same location as the epifaunal samples. Initially, 10 cores for infauna were taken with a plexiglas corer (0.007 m^2) to a depth of 15 cm. Subsequently, it was found that seven cores were adequate to describe the density and diversity of infauna. Infaunal cores were placed in labeled plastic bags containing isotonic $MgCl_2$ as a relaxant. This prevented smaller polychaetes and oligochaetes from crawling through the sieve. All infaunal samples were washed through a 0.5 mm mesh sieve and then retained material was preserved in 10% buffered seawater and formalin. Rose Bengal was also used to facilitate laboratory sorting.

All individuals were identified to species if possible using the most recent keys for identifying marine invertebrates.

Three sediment cores were taken from each treatment each sampling period and sediment grain size analysis conducted on each sample according to Folk (1961).

Sediment traps, consisting of three small jars strapped to a wooden top with funnels clamped to the wooden top to allow suspended sediments to accumulate in the jar, were used to assess any differences in sedimentation rates in the pens and cages in the sand area only.

Dyed sediments were placed inside the pen and cages both in the grass and sand area to monitor sediment mobility in each of these treatments.

Larval traps, made of one gallon jars attached to stakes inside and outside pens, were also used to assess variations in larval recruitment rates that may be due to cage effects.

Because of the excess fouling that can occur on exposed objects, the pens and cages were cleaned regularly to prevent buildup of excessive epiphytic algae by rubbing all sides with plastic cloth brushes constructed of the same material the cages were made of.

Minnow traps and small crab pots were maintained inside each of the pens to catch small fish and crabs that may have entered the pen at small sizes and grown to sizes where they could not exit. Cages were examined weekly to remove fish or crabs that entered the cages.

Numerical abundance histograms were plotted by area for both species and individuals found in the infaunal and epifaunal (grass bed only) community. Species diversity was calculated for each area using the index of Shannon (Pielou, 1975). The index H' is expressed as:

$$H' = \sum_{i-=1}^{s} Pi \log_2 Pi$$

where s = number of species on the sample and Pi = proportion of the i-th species in the sample. This index is commonly used for comparative purposes and includes both a species richness (the number of species in a community) component and an evenness (how equitably the individuals are distributed between the species) component.

Because the blue crab, *Callinectes sapidus* is such a dominant predator in the grass bed, we examined the stomachs of blue crabs for feeding analysis. Eighty-three blue crab stomachs were analyzed in 1978. Individuals were collected with a 4.87 m (16 ft) otter trawl with 19 mm (3/4 inch) wings and a 6.3 mm (1/4 inch) cod end liner. The trawl was pulled for a period of 2 min. at a speed of 2 to 3 knots. Collected crabs were subsampled and those selected were immediately weighed, measured, sexed, and the molt stage noted. Stomachs were removed in the field and preserved in 10% buffered seawater formalin with the vital stain, Rose Bengal. Each stomach was carefully dissected in the laboratory and the contents enumerated and identified when possible.

RESULTS

The pen and cage experiments in the sand and grass areas affected both the epifaunal and infaunal components during the course of this study. Because of the large data set collected for both components, the results for the infauna and epifauna will be presented separately. It must be stressed that this separation is artificial and done only for simplification of the discussion. However, there are undoubtedly important interactions that occur between both components and any possible interaction will be analyzed in the discussion section.

I. Infauna

Despite the cages and pens being present for only two months, there were some dramatic differences in the response of the infauna to several of the treatments.

In comparing the sand area to the grass area for the June data, several effects were evident: 1. The mean number of species per core for all the treatments in grass were higher than the comparable treatments in sand (Fig. 3). Within the grass area, there were no differences among the treatments whereas in the sand, the cage (C) and pen + cage (PC) treatments had more species than the other treatments. The pen (P) and pen + open cage (PO), in turn, had more species than the control (S) and open cage (O). 2. The mean number of individuals per core for the grass treatments were greater than the sand treatments except for the cage (C) and pen + cage treatment (PC) (Fig. 4), where similar numbers were recorded. There were no differences among all of the grass treatments whereas the sand cage (C) and pen + cage (PC) were greater than the other four sand treatments. 3. Comparison of diversity between the two habitats (Fig. 5) was not as distinct as with number of species or individuals since the H' index is sensitive to not only species number but the distribution of the individuals among those species. Diversity was, in general, highest in the grass areas as compared to the sand area, with the pen + (PC) cage treatment having the highest diversity of the sand treatments. Lowest diversity was found for the sand control (S) and open cage (O) in the sand area. 4. The pattern of species dominance was very different for the sand and grass habitats (Table 1, 2). This was particularly evident for the soft shell clam, *Mya arenaria*, whose high densities only in the sand cage (C) and sand cage + pen (P+C), contributed to the high densities of individuals for these two treatments. *Gemma gemma* was also found in increased abundance in these two treatments as compared to the other sand treatments. *Gemma* was the dominant species in the other sand treatments but densities were not as high in the cage treatments. The grass infauna was dominated by large numbers of the capitellid polychaete, *Heteromastus filiformis*, the spionid polychaetes, *Polydora ligni* and *Streblospio benedicti*, and oligochaetes. The cirriped, *Balanus improvisus*, was recorded in these samples. Though *Balanus* is epifaunal, many were present on old leaf material that had settled on the bottom after the barnacle covered leaves had sloughed off from the plants. *Mya arenaria* was present in the grass treatments but their numbers were low compared with the densities found in several of the cage treatments. Many of the dominant grass infaunal species were present in the sand area but in very low densities and there were no species that were restricted to either of the two habitats.

Data for the September sampling date revealed similar trends to the June data: 1. There were more species in the grass habitat than the sand (Fig. 3). The numbers of species per core for the pen (P) and cage (C') treatments in the sand were not different from each other but were higher than the control. The species per core in the

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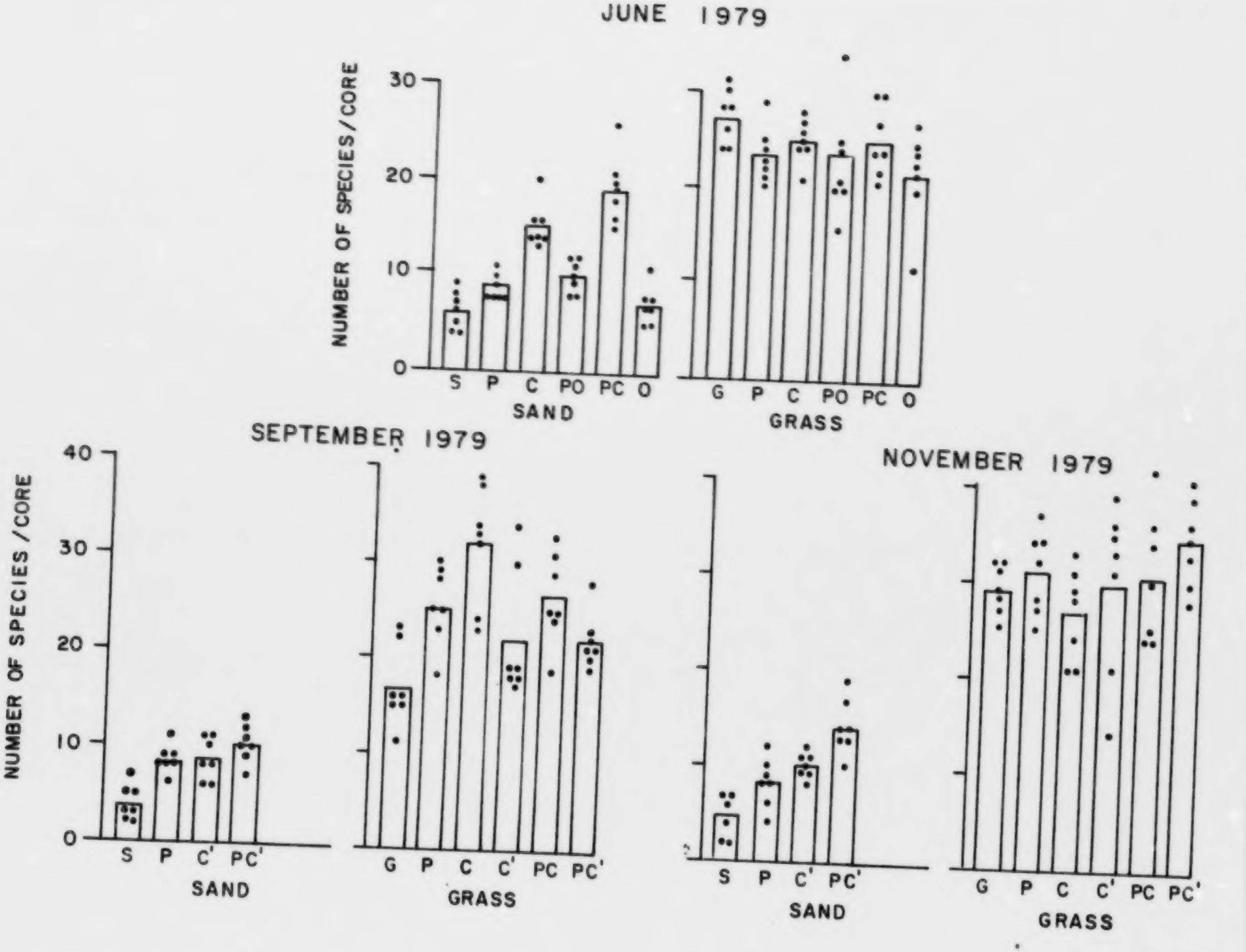

Fig. 3. Number of species per core recorded from infaunal samples for all treatments each sampling period. Treatment designations are as follows: S=sand control; G=grass control; P=pen; C=cage; PO=pen + open cage; PC=pen + cage; O=open cage, 2 sides and no top; C'=new cage set in June; PC'=new pen + cage set in June. Closed circles (·) represent number of species for the cores taken for each treatment. Boxes represent mean number of species per core.

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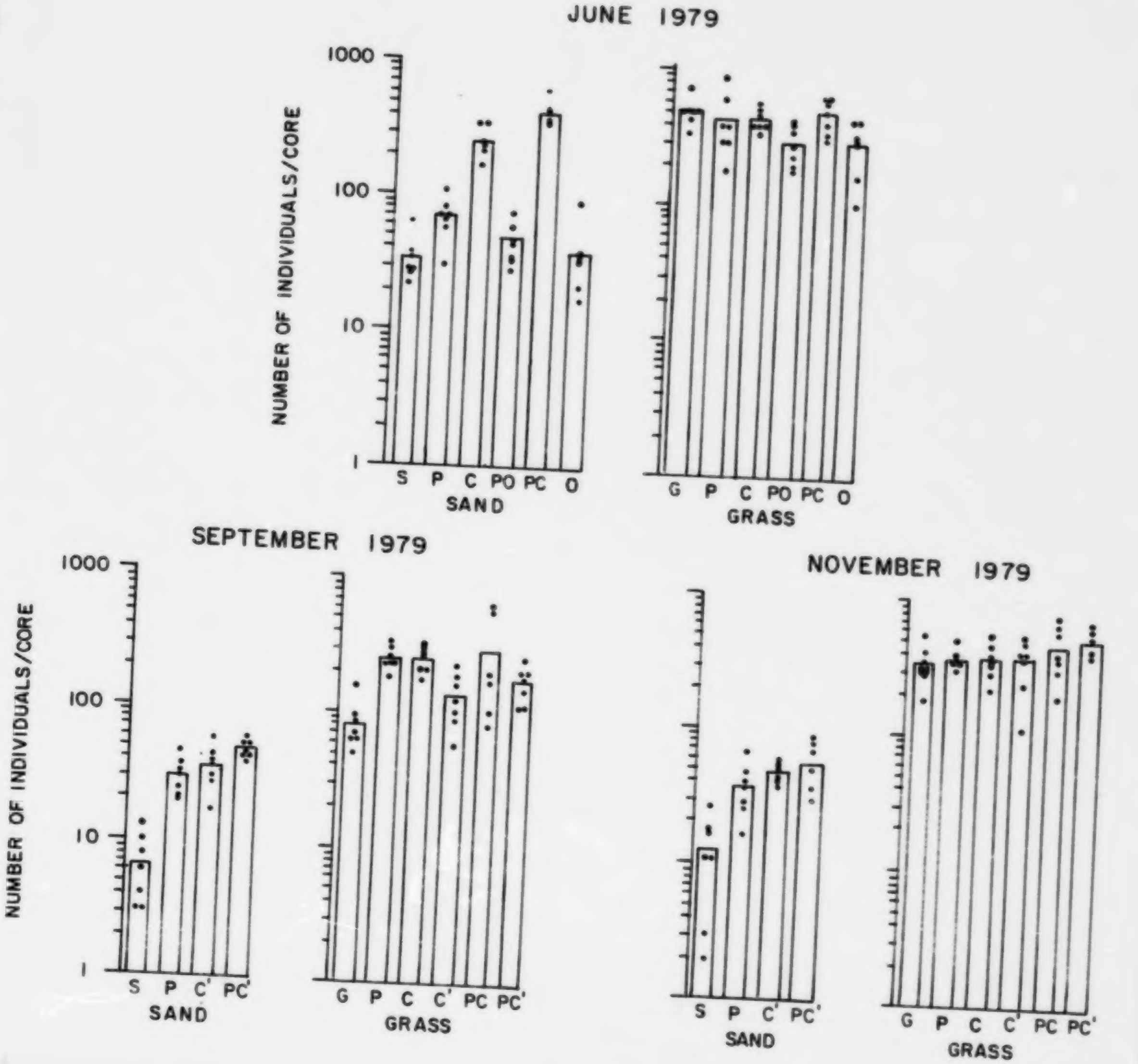

Fig. 4. Number of individuals per core recorded from infaunal samples for all treatment each sampling period. Treatment designations are as follows: S=sand control; G=grass control; P=pen; C=cage; PO= pen + open cage; PC=pen + cage; O=open cage, 2 sides and no top; C'=new cage set in June; PC'=new pen + cage set in June. Closed circles (·) represent number of individuals for the cores taken for each treatment. Boxes represent mean number of individuals per core.

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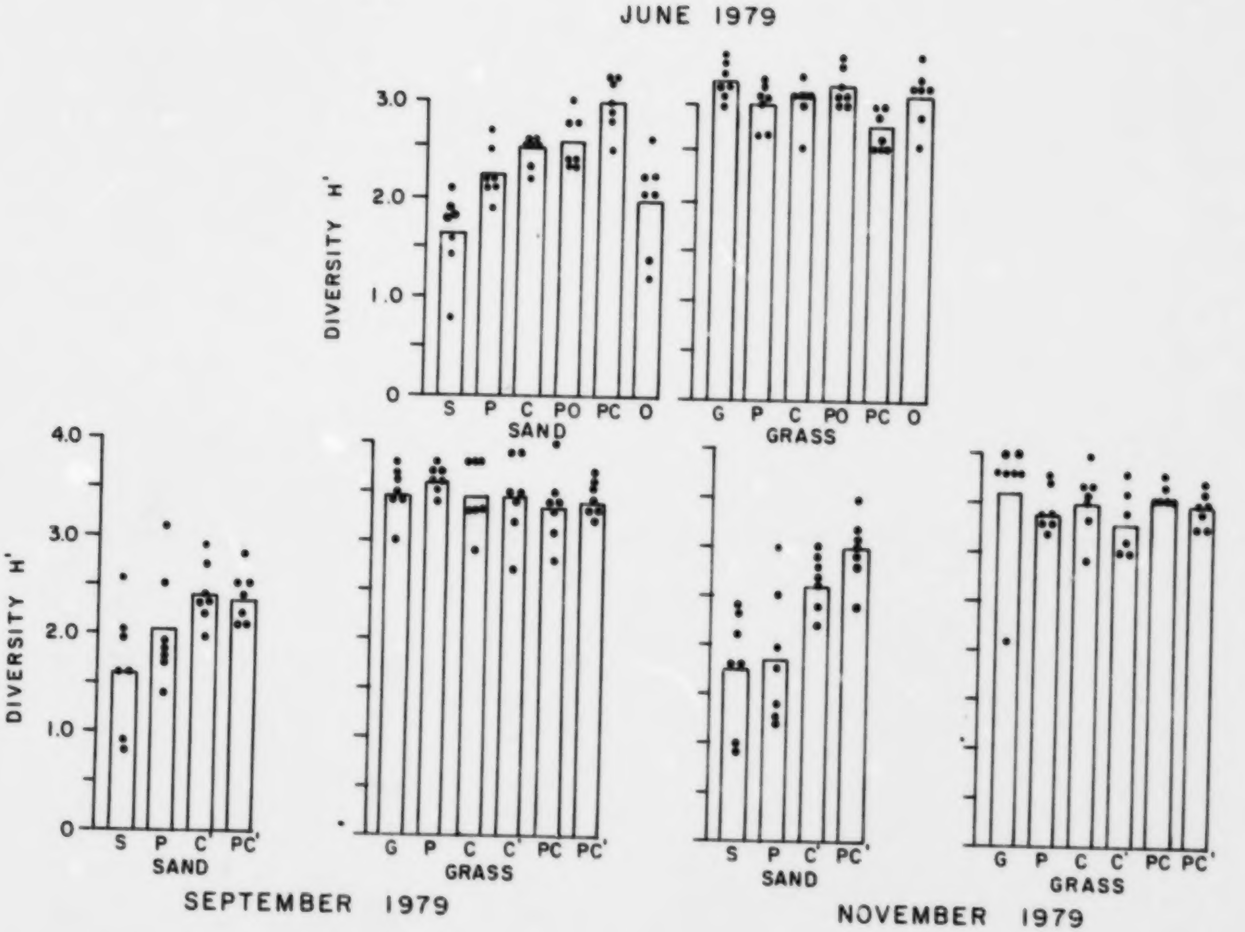

Fig. 5. Diversity (H') values for infaunal species from all treatments each sampling period. Treatment designations are as follows: S=sand control; G=grass control; P=pen; C=cage; PO=pen + open cage; PC=pen + cage; O=open cage, 2 sides and no top; C'=new cage set in June; PC'=new pen + cage set in June. Closed circles (·) represents diversity values calculated for each core in each treatment. Boxes represent the mean diversity value for seven cores for that treatment.

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TABLE 1. LIST OF TOP TEN DOMINANT SPECIES RECORDED FROM INFAUNAL CAGING EXPERIMENT SAMPLES FOR THE SAND HABITAT FOR JUNE. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE AND ITS DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

INSIDE SAND

Species	$^o/_o$	$\#/m^2$
1. *Gemma gemma*	57.02	2857.14
2. *Oligochaeta*	14.05	703.93
3. *Scolecolepides viridis*	7.85	393.37
4. *Capitella capitata*	4.55	227.74
5. *Heteromastus filiformis*	3.72	186.34
6. *Scolelepis squamata*	3.31	165.63
7. *Mya arenaria*	2.89	144.93
8. *Gastropoda*	1.65	82.82
9. *Haminoea solitaria*	1.24	62.11
10. *Polydora ligni*	0.83	41.41
Total	97.11	4865.42
Total sample	100.00	5010.35

CAGE

Species	$^o/_o$	$\#/m^2$
1. *Mya arenaria*	43.41	16583.86
2. *Gemma gemma*	15.12	5776.40
3. *Heteromastus filiformis*	14.15	5403.73
4. *Streblospio benedicti*	13.22	5051.76
5. *Mulinia lateralis*	2.66	1014.49
6. *Polydora ligni*	2.55	973.09
7. *Cistena gouldii*	2.38	910.97
8. *Nereis succinea*	1.36	517.60
9. *Odostomia bisuturalis*	0.81	310.56
10. *Capitella capitata*	0.60	227.74
Total	96.26	36770.20
Total sample	100.00	38198.75

OPEN CAGE

Species	$^o/_o$	$\#/m^2$
1. *Gemma gemma*	55.23	3167.70
2. *Heteromastus filiformis*	10.47	600.41
3. *Capitella capitata*	9.03	517.60
4. *Mya arenaria*	8.30	476.19
5. *Scolecolepides viridis*	3.97	227.74
6. *Odostomia bisuturalis*	2.89	165.68
7. *Polydora ligni*	2.53	144.93
8. *Haminoea solitaria*	2.17	124.22
9. *Streblospio benedicti*	1.44	82.82
10. *Balanus improvisus*	1.44	82.82
Total	97.47	5590.11
Total sample	100.00	5734.99

PEN

Species	$^o/_o$	$\#/m^2$
1. *Gemma gemma*	38.11	3850.93
2. *Mya arenaria*	28.60	2898.55
3. *Heteromastus filiformis*	14.75	1490.68
4. *Tharyx setigera*	4.92	496.89
5. *Scolecolepides viridis*	4.30	434.78
6. *Capitella capitata*	1.43	144.93
7. *Odostomia* sp.	1.43	144.93
8. *Streblospio benedicti*	1.23	124.22
9. *Balanus improvisus*	1.02	103.52
10. *Polydora ligni*	0.61	62.11
Total	96.49	9751.54
Total sample	100.00	10103.52

CAGE + PEN

Species	$^o/_o$	$\#/m2$
1. *Mya arenaria*	31.05	19151.14
2. *Gemma gemma*	14.10	8695.65
3. *Streblospio benedicti*	13.53	8343.69
4. *Heteromastus filiformis*	8.93	5507.25
5. *Hamincea solitaria*	8.76	5403.73
6. *Mulinia lateralis*	4.73	2919.26
7. *Polydora ligni*	3.93	2422.36
8. *Cistena gouldii*	3.63	2236.03
9. *Nereis succinea*	2.35	1449.28
10. *Odostomia*	1.24	766.05
Total	92.25	56894.44
Total sample	100.00	61676.98

OPEN CAGE + PEN

Species	$^o/_o$	$\#/m^2$
1. *Gemma gemma*	24.92	1718.43
2. *Heteromastus filiformis*	24.62	1697.72
3. *Streblospio benedicti*	10.51	724.64
4. *Tharyx setigera*	8.71	600.41
5. *Scolecolepides viridis*	6.61	455.49
6. *Mya arenaria*	6.01	414.08
7. *Prionospio heterobranchia*	3.90	269.15
8. *Phoronis architecta*	3.30	227.74
9. *Balanus improvisus*	3.00	207.04
10. *Glycera dibranchiata*	1.20	82.82
Total	92.78	6397.52
Total sample	100.00	6894.41

TABLE 2. LIST OF TOP TEN DOMINANT SPECIES RECORDED FROM INFAUNAL CAGING EXPERIMENT SAMPLES FROM THE GRASS HABITAT FOR JUNE. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE AND ITS DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

MIXED

Species	$^o/_o$	#/m^2
1. *Heteromastus filiformis*	27.94	20041.41
2. *Balanus improvisus*	24.16	17329.20
3. *Oligochaeta*	8.72	6252.59
4. *Polydora ligni*	8.00	5734.00
5. *Streblospio benedicti*	6.44	4616.98
6. *Nereis succinea*	4.01	2877.85
7. *Gemma gemma*	3.26	2339.55
8. *Edotea triloba*	2.60	1863.35
9. *Erichsonella attenuata*	2.48	1780.54
10. *Mya arenaria*	2.45	1759.83
Total	90.06	64595.30
Total sample	100.00	71718.38

CAGE

Species	$^o/_o$	#/m^2
1. *Heteromastus filiformis*	33.77	21946.18
2. *Streblospio benedicti*	24.08	15652.18
3. *Balanus improvisus*	9.46	6149.07
4. *Polydora ligni*	5.83	3788.82
5. *Mya arenaria*	3.95	2567.29
6. *Eteone heteropoda*	3.50	2277.43
7. *Oligochaeta*	2.96	1925.47
8. *Nereis succinea*	2.55	1656.32
9. *Gemma gemma*	1.72	1118.01
10. *Erichsonella attenuata*	1.62	1055.90
Total	89.44	58136.67
Total sample	100.00	64989.65

OPEN CAGE

Species	$^o/_o$	#/m^2
1. *Balanus improvisus*	25.33	11573.50
2. *Heteromastus filiformis*	25.10	11469.98
3. *Streblospio benedicti*	9.61	4389.23
4. *Polydora ligni*	8.84	4037.27
5. *Gemma gemma*	6.80	3105.59
6. *Oligochaeta*	4.17	1904.76
7. *Erichsonella attenuata*	3.76	1718.43
8. *Nereis succinea*	3.72	1697.72
9. *Mya arenaria*	2.54	1159.42
10. *Edotea triloba*	1.72	786.75
Total	91.59	43623.19
Total sample	100.00	45693.55

PEN

Species	$^o/_o$	#/m^2
1. *Heteromastus filiformis*	31.09	19958.60
2. *Balanus improvisus*	18.25	11718.43
3. *Oligochaeta*	12.96	8322.98
4. *Streblospio benedicti*	11.90	7639.75
5. *Polydora ligni*	8.06	5175.98
6. *Nereis succinea*	3.48	2236.03
7. *Mya arenaria*	2.26	1449.28
8. *Edotea triloba*	2.13	1366.46
9. *Erichsonella attenuata*	2.10	1345.76
10. *Scoloplos*	1.19	766.05
Total	93.42	59979.32
Total sample	100.00	64202.88

CAGE + PEN

Species	$^o/_o$	#/m^2
1. *Balanus improvisus*	35.89	25838.52
2. *Heteromastus filiformis*	25.45	18322.98
3. *Streblospio benedicti*	13.17	9482.40
4. *Polydora ligni*	7.51	5403.73
5. *Oligochaeta*	3.94	2836.44
6. *Mya arenaria*	3.22	2318.84
7. *Nereis succinea*	1.52	1097.31
8. *Gemma gemma*	1.21	869.57
9. *Erichsonella attenuata*	1.21	869.57
10. *Scoloplos*	0.86	621.12
Total	93.98	67657.48
Total sample	100.00	71987.50

OPEN CAGE PEN

Species	$^o/_o$	#/m^2
1. *Heteromastus filiformis*	29.38	12857.14
2. *Streblospio benedicti*	15.23	6666.67
3. *Balanus improvisus*	15.23	6666.67
4. *Polydora ligni*	10.65	4679.09
5. *Oligochaeta*	4.59	2008.28
6. *Edotea triloba*	4.49	1966.87
7. *Nereis succinea*	3.64	1594.20
8. *Mya arenaria*	3.07	1345.76
9. *Erichsonella attenuata*	2.60	1138.72
10. *Eteone heteropoda*	1.70	745.34
Total	90.62	39668.74
Total sample	100.00	43768.06

grass treatments were variable as evidenced by the distribution of each of the cores for each treatment. The mean number of species per core for the older cage (C) and pen + cage (PC) treatments were greater than the other treatments while the grass control (G) had the fewest but these are probably not significantly different. Species number was reduced in the control as compared to the June data while the new cage (C') and pen + cage (PC') treatments had less mean number of species per core than the comparable older treatments. 2. Numbers of individuals were again higher in the grass habitat than the sand but the differences were not as large as in June. The density of infauna for the sand treatments were greater than the control as was the case for the grass habitat. The density of infauna in the grass control (G) was also similar to the sand treatments. Overall, densities of infauna in the grass and sand were less than that observed in June for all treatments. 3. Mean diversity (H') was higher in the grass habitat than in the sand habitat. There was no difference among the grass treatments and control while in the sand, H' was higher in the treatments than the control though there was considerable overlap of the H' for the samples. 4. Dominance patterns of species in each of the two habitats for the different treatments varied from the previous sampling period (Tables 3, 4). Because the caged areas in the sand were completely disturbed, after the June sampling by blue crabs, the pattern represent trends recorded for only two months. The grass cages, because they were not disturbed, allowed for a comparison over a longer time scale. In addition, the newer cages, also set up in June to compliment the sand studies, allowed comparisons of recruitment on a shorter time scale. In the sand area, the bivalve Gemma gemma was one of the dominant species (Table 3) in the pen (P) and cage treatments (C', PC') but was absent from the control area (S). Species present in the control area were only small, tube dwelling polychaetes in very low abundances. Another bivalve, Mulinia lateralis, was only abundant in the cage (C') and pen + cage (PC') treatments. In the grass treatments (Table 4) Gemma was very abundant, whose densities were, in most cases, higher than those densities recorded in June. The polychaete, Heteromastus filiformis, was much less abundant in June, though it was still one of the top 10 species. Balanus was no longer a dominant species (except in the old cage (C), a result of the old leaves having either been washed out of the area or dying as the leaves to which they were attached decayed. Oligochaetes were also abundant as they were in June with approximately similar densities (one exception, they were not dominant in the cage treatment).

One particularly interesting species found more abundantly in the caged treatments, especially those initiated in April (C and PC) than the pen (P) or control (G) was the oyster, Crassostrea virginica (Table 5). Crassostrea is usually not found setting in grass beds but was found to have actually set on pieces of eelgrass along the bottom of the cages.

Crepidula convexa, an epifaunal gastropod was abundant in all the treatments. Its presence as an infaunal component is a reflection,

TABLE 3. LIST OF TOP TEN DOMINANT SPECIES RECORDED FROM INFAUNAL CAGING EXPERIMENT SAMPLES FROM THE SAND HABITAT FOR SEPTEMBER. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE AND ITS DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

INSIDE SAND

Species	°/o	#/m^2
1. *Capitella capitata*	40.43	393.37
2. *Heteromastus filiformis*	14.89	144.93
3. *Oligochaeta*	8.51	82.82
4. *Scolelepis squamata*	6.38	62.11
5. *Streblospio benedicti*	6.38	62.11
6. *Ampithoe longimana*	6.38	62.11
7. *Paraprionospio pinnata*	4.26	41.41
8. *Glycinde solitaria*	2.13	20.70
9. *Polydora ligni*	2.13	20.70
10. *Scolecolepides viridis*	2.13	20.70
Total	93.59	910.96
Total sample	100.00	973.08

CAGE (NEW SET)

Species	°/o	#/m^2
1. *Nereis succinea*	33.59	1780.54
2. *Gemma gemma*	14.06	745.34
3. *Mulinia lateralis*	13.67	724.64
4. *Capitella capitata*	12.89	683.23
5. *Oligochaeta*	5.47	289.85
6. *Glycinde solitaria*	4.30	227.74
7. *Scoloplos*	3.91	207.04
8. *Polydora ligni*	3.13	165.63
9. *Cyclaspis varians*	2.34	124.22
10. *Streblospio benedicti*	1.56	82.82
Total	94.92	3031.05
Total sample	100.00	5300.20

PEN

Species	°/o	#/m^2
1. *Gemma gemma*	60.75	2691.51
2. *Retusa canaliculata*	8.88	393.37
3. *Heteromastus filiformis*	5.14	227.74
4. *Phoronis architecta*	3.27	144.93
5. *Edotea triloba*	2.80	124.22
6. *Capitella capitata*	2.34	103.52
7. *Gyptis vittata*	1.87	82.82
8. *Glycera dibranchiata*	1.87	82.82
9. *Cyclaspis varians*	1.87	82.82
10. *Nereis succinea*	1.40	62.11
Total	90.19	3995.86
Total sample	100.00	4430.64

PEN + CAGE (NEW SET)

Species	°/o	#/m^2
1. *Gemma gemma*	48.24	3395.45
2. *Mulinia lateralis*	16.18	1138.72
3. *Heteromastus filiformis*	10.59	745.34
4. *Nereis succinea*	5.59	393.37
5. *Gyptis vittata*	1.47	103.52
6. *Scoloplos*	1.47	103.52
7. *Crepidula convexa*	1.47	103.52
8. *Retusa canaliculata*	1.47	103.52
9. *Edotea triloba*	1.47	103.52
10. *Glycera dibranchiata*	1.18	82.82
Total	89.13	6273.30
Total sample	100.00	7039.34

TABLE 4. LIST OF TOP TEN DOMINANT SPECIES RECORDED FROM INFAUNAL CAGING EXPERIMENT SAMPLES FROM THE GRASS HABITAT FOR SEPTEMBER. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE AND ITS DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

MIXED

Species	°/o	#/m^2
1. Nereis succinea	19.17	2298.14
2. Gemma gemma	15.54	1863.35
3. Oligochaeta	10.36	1242.24
4. Erichsonella attenuata	8.12	973.09
5. Heteromastus filiformis	7.43	890.27
6. Cymadusa compta	6.56	786.75
7. Spiochaetopterus oculatus	4.66	559.01
8. Edotea triloba	4.32	517.60
9. Crepidula convexa	3.45	414.08
10. Scoloplos	3.28	393.37
Total	82.89	9937.90
Total sample	100.00	11987.58

CAGE

Species	°/o	#/m^2
1. Gemma gemma	35.13	13354.09
2. Nereis succinea	14.43	5486.54
3. Crassostrea virginica	9.37	3561.08
4. Balanus improvisus	5.12	1946.17
5. Crepidula convexa	5.01	1904.76
6. Heteromastus filiformis	2.83	1076.60
7. Oligochaeta	2.78	1055.90
8. Polydora ligni	2.40	910.97
9. Mulinia lateralis	2.07	786.75
10. Scoloplos	2.02	766.05
Total	81.16	30848.91
Total sample	100.00	38012.42

CAGE(NEW)

Species	°/o	#/m^2
1. Gemma gemma	19.90	3995.86
2. Nereis succinea	15.46	3105.59
3. Crepidula convexa	14.64	2939.96
4. Crassostrea virginica	8.76	1759.83
5. Cymadusa compta	7.01	1407.87
6. Spiochaetopterus oculatus	4.12	828.16
7. Mulinia lateralis	3.51	703.93
8. Polydora ligni	2.89	579.71
9. Heteromastus filiformis	2.47	496.89
10. Sabellaria vulgaris	2.47	496.89
Total	76.23	16314.69
Total sample	100.00	20082.82

PEN

Species	°/o	#/m^2
1. Crepidula convexa	21.92	8302.28
2. Edotea triloba	11.92	4513.46
3. Oligochaeta	11.86	4492.75
4. Gemma gemma	11.04	4182.20
5. Nereis succinea	7.93	3002.07
6. Erichsonella attenuata	7.93	3002.07
7. Spiochaetopterus oculatus	3.17	1200.83
8. Cymadusa compta	3.17	1200.83
9. Heteromastus filiformis	3.12	1180.12
10. Mediomastus ambiseta	2.41	910.97
Total	84.47	31987.58
Total sample	100.00	37867.46

CAGE + PEN

Species	°/o	#/m^2
1. Mulinia lateralis	24.35	10621.12
2. Crassostrea virginica	24.36	10621.12
3. Crepidula convexa	17.42	7598.34
4. Oligochaeta	5.93	2587.99
5. Nereis succinea	5.51	2401.66
6. Gemma gemma	2.71	1180.12
7. Spiochaetopterus oculatus	2.23	973.09
8. Mediomastus ambiseta	1.95	848.86
9. Cymadusa compta	1.52	662.53
10. Edotea triloba	1.14	496.89
Total	87.11	37991.72
Total sample	100.00	43623.17

PEN & CAGE (NEW SET)

Species	°/o	#/m^2
1. Oligochaeta	17.70	4679.09
2. Crepidula convexa	16.44	4347.82
3. Nereis succinea	14.88	3933.75
4. Gemma gemma	9.08	2401.66
5. Spiochaetopterus oculatus	6.97	1842.65
6. Mediomastus ambiseta	5.79	1532.09
7. Crassostrea virginica	5.64	1490.68
8. Heteromastus filiformis	5.25	1387.16
9. Cymadusa compta	2.51	662.53
10. Glycinde solitaria	1.72	455.49
Total	85.98	22732.92
Total sample	100.00	26438.93

TABLE 5. DENSITIES (PER M^2) OF THE OYSTER, CRASSOSTREA VIRGINICA, FOUND IN THE GRASS HABITAT FOR EACH OF THE EXPERIMENTAL TREATMENTS AND CONTROL FOR SEPTEMBER AND NOVEMBER.

	September	November
Control (G)	21	41
Old cage (C)	3561	4265
New cage (C')	1760	-
Pen (P)	642	104
Pen + old cage (PC)	10621	9317
Pen + new cage (PC')	1491	1222

probably, of its spillover from the epifauna where it was present in very large numbers.

The patterns discussed above for the infauna collected in June and September was evident in most cases through November. 1. The number of species was again higher in the grass habitat compared with the sand habitat (Fig. 3). Species number was higher in the sand treatments compared with the control while in the grass, there were no distinct differences among the treatments, although there was a lot of variation between cores of similar treatments. Except for the old cage treatment, the mean number of species for each of the grass treatments and control was higher compared to September and in June. 2. The number of individuals per core was higher in all grass treatments compared with the sand treatments (Fig. 4). Density in the sand control was less than the three experimental treatments which among themselves were not different. Densities in the grass treatments were similar and were higher than densities found in the grass habitat in September. 3. Diversity (H') was also higher in the grass habitats compared to the sand area. The sand treatments incorporating the cages had a higher H' than the pen or control while the mean diversity for each grass treatment was not different. 4. The dominant species in the sand area in November was similar to that found in September (Table 6). Gemma was the dominant species in the pen + cage (PC'), pen (P), and new cage (C') treatments and Capitella (polychaete) was dominant in the control (S) with Gemma the second most abundant species. The spionid polychaetes, Streblospio and Polydora, increased in abundances over the September densities.

Species dominance in the grass treatments for November (Table 7) were, in most cases, not similar to each other. Gemma was the dominant species in the new cage (C') as it was in September and was also abundant in the pen + new cage (PC'), pen (P) and grass control (G). Densities of Crassostrea (Table 5) were similar to that recorded in September for the new cage (C') and was also very abundant in the old cage (C) and pen + new cage (PC') treatments. It was not recorded in the new cage treatment (C') where, in September, the new cage contained 1760/m^2. Crepidula was still abundant in all treatments and control. The oligochaetes increased in density over September's density in the new cage (C'), grass control, old cage + pen (PC) and old cage (C). Densities of Polydora ligni and Streblospio benedicti increased in all treatments compared with September as was the case for the sand treatments discussed above.

II. Epifauna

Because of the experimental design, only one sample of eelgrass could be taken at the time of sampling. All samples were roughly estimated to be approximately 0.1 m^2 in order to make sample size equivalent.

In June, the penned treatments (P, PO and PC) had more species per sample (Fig. 6) than the unpenned area while the caged area (C)

TABLE 6. LIST OF TOP TEN DOMINANT SPECIES RECORDED FROM INFAUNAL CAGING EXPERIMENT SAMPLES FROM THE SAND HABITAT FOR NOVEMBER. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE AND ITS DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

INSIDE SAND

Species	°/o	#/m^2
1. *Capitella capitata*	42.70	786.75
2. *Gemma gemma*	17.98	331.26
3. *Streblospio benedicti*	11.24	207.04
4. *Scolelepis squamata*	7.87	144.93
5. *Rhyncocoela*	5.62	103.52
6. *Heteromastus filiformis*	5.62	103.52
7. *Hargeria rapax*	3.37	62.11
8. *Spiochaetopterus oculatus*	1.12	20.70
9. *Retusa canaliculata*	1.12	20.70
10. *Neomysis americana*	1.12	20.70
Total	97.76	1801.23
Total sample	100.00	1842.65

CAGE (NEW)

Species	°/o	#/m^2
1. *Gemma gemma*	32.28	2318.84
2. *Streblospio benedicti*	24.78	1780.54
3. *Saccoglossus kowalewskii*	10.66	766.05
4. *Capitella capitata*	8.36	600.41
5. *Polydora ligni*	6.63	476.19
6. *Oxyurostylis smithi*	4.03	289.85
7. *Heteromastus filiformis*	2.31	165.63
8. *Odostomia*	2.31	165.63
9. *Oligochaeta*	1.15	82.82
10. *Hargeria rapax*	1.15	82.82
Total	93.66	6728.78
Total sample	100.00	7184.26

PEN

Species	°/o	#/m^2
1. *Gemma gemma*	66.29	3664.60
2. *Retusa canaliculata*	9.36	517.60
3. *Odostomia*	5.62	310.56
4. *Heteromastus filiformis*	3.00	165.63
5. *Streblospio benedicti*	3.00	165.63
6. *Spiochaetopterus oculatus*	1.87	103.52
7. *Capitella capitata*	1.50	82.82
8. *Stylochus ellipticus*	1.50	82.82
9. *Scolelepis squamata*	1.12	62.11
10. *Phoronis architecta*	1.12	62.11
Total	94.38	5217.40
Total sample	100.00	5527.95

PEN + CAGE (NEW SET)

Species	°/o	#/m^2
1. *Gemma gemma*	35.90	2898.55
2. *Streblospio benedicti*	18.21	1469.98
3. *Polydora ligni*	7.18	579.71
4. *Heteromastus filiformis*	6.15	496.89
5. *Spiochaetopterus oculatus*	4.62	372.67
6. *Ostracoda*	3.08	248.45
7. *Scoloplos*	2.82	227.74
8. *Phoronis architecta*	2.82	227.74
9. *Gyptis brevipalpa*	2.31	186.34
10. *Nereis succinea*	1.79	144.93
Total	84.88	6853.00
Total sample	100.00	5074.53

TABLE 7. LIST OF TOP TEN DOMINANT SPECIES RECORDED FROM INFAUNAL CAGING EXPERIMENT SAMPLES FROM THE GRASS HABITAT FOR NOVEMBER. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE AND ITS DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

MIXED

Species	°/o	#/m^2
1. *Oligochaeta*	28.55	14409.94
2. *Polydora ligni*	14.89	7515.53
3. *Nereis succinea*	9.60	4844.72
4. *Mediomastus ambiseta*	6.81	3436.85
5. *Crepidula convexa*	5.82	9239.96
6. *Heteromastus filiformis*	4.18	2111.80
7. *Brania clavata*	3.90	1966.87
8. *Gemma gemma*	3.69	1863.35
9. *Streblospio benedicti*	3.12	1573.50
10. *Spiochaetopterus oculatus*	2.87	1449.28
Total	83.43	48411.80
Total sample	100.00	50476.16

CAGE

Species	°/o	#/m^2
1. *Oligochaeta*	22.37	12360.25
2. *Mulinia lateralis*	12.10	6687.37
3. *Mediomastus ambiseta*	10.04	5548.65
4. *Crassostrea virginica*	7.72	4265.01
5. *Crepidula convexa*	6.41	3540.37
6. *Polydora ligni*	5.70	3147.00
7. *Gyptis brevipalpa*	4.65	2567.29
8. *Brania clavata*	4.12	2277.43
9. *Paracaprella tenuis*	3.37	1863.35
10. *Montacuta elevata*	3.37	1863.35
Total	79.85	44120.07
Total sample	100.00	55258.77

CAGE (NEW)

Species	°/o	#/m^2
1. *Gemma gemma*	26.32	14761.91
2. *Mediomastus ambiseta*	20.52	11511.39
3. *Crepidula convexa*	15.02	8426.50
4. *Oligochaeta*	7.38	4140.79
5. *Polydora ligni*	7.24	4057.76
6. *Streblospio benedicti*	2.99	1677.02
7. *Heteromastus filiformis*	2.95	1656.32
8. *Nereis succinea*	2.88	1614.91
9. *Brania clavata*	1.96	1097.31
10. *Spiochateopterus oculatus*	1.77	993.79
Total	89.03	49937.70
Total sample	100.00	56086.94

PEN

Species	°/o	#/m^2
1. *Gemma gemma*	26.32	14761.91
2. *Mediomastus ambiseta*	20.52	11511.39
3. *Crepidula convexa*	15.02	8426.50
4. *Oligochaeta*	7.38	4140.79
5. *Polydora ligni*	7.24	4057.97
6. *Streblospio benedicti*	2.99	1677.02
7. *Heteromastus filiformis*	2.95	1656.32
8. *Nereis succinea*	2.88	1614.91
9. *Brania clavata*	1.96	1097.31
10. *Spiochaetopterus oculatus*	1.77	993.79
Total	89.03	49937.91
Total sample	100.00	56086.94

CAGE + PEN

Species	°/o	#/m^2
1. *Crepidula convexa*	33.92	18053.34
2. *Mediomastus ambiseta*	9.06	4824.02
3. *Polydora ligni*	8.13	4327.12
4. *Nereis succinea*	8.05	4825.71
5. *Gemma gemma*	7.86	4182.20
6. *Oligochaeta*	5.72	3043.48
7. *Streblospio benedicti*	5.56	2960.66
8. *Spiochaetopterus oculatus*	3.89	2070.39
9. *Erichsonella attenuata*	2.10	1118.01
10. *Brania clavata*	2.02	1076.60
Total	86.31	46481.53
Total sample	100.00	53229.79

PEN + CAGE (NEW SET)

Species	°/o	#/m^2
1. *Crepidula convexa*	26.24	20766.05
2. *Gemma gemma*	17.48	13830.23
3. *Mediomastus ambiseta*	12.32	9751.55
4. *Polydora ligni*	9.05	7163.56
5. *Nereis succinea*	5.94	4699.79
6. *Oligochaeta*	5.47	4327.12
7. *Streblospio benedicti*	4.89	3871.64
8. *Brania clavata*	4.24	3354.04
9. *Spiochaetopterus oculatus*	1.70	1345.76
10. *Crassostrea virginica*	1.54	1221.53
Total	88.87	70331.27
Total sample	100.00	79130.38

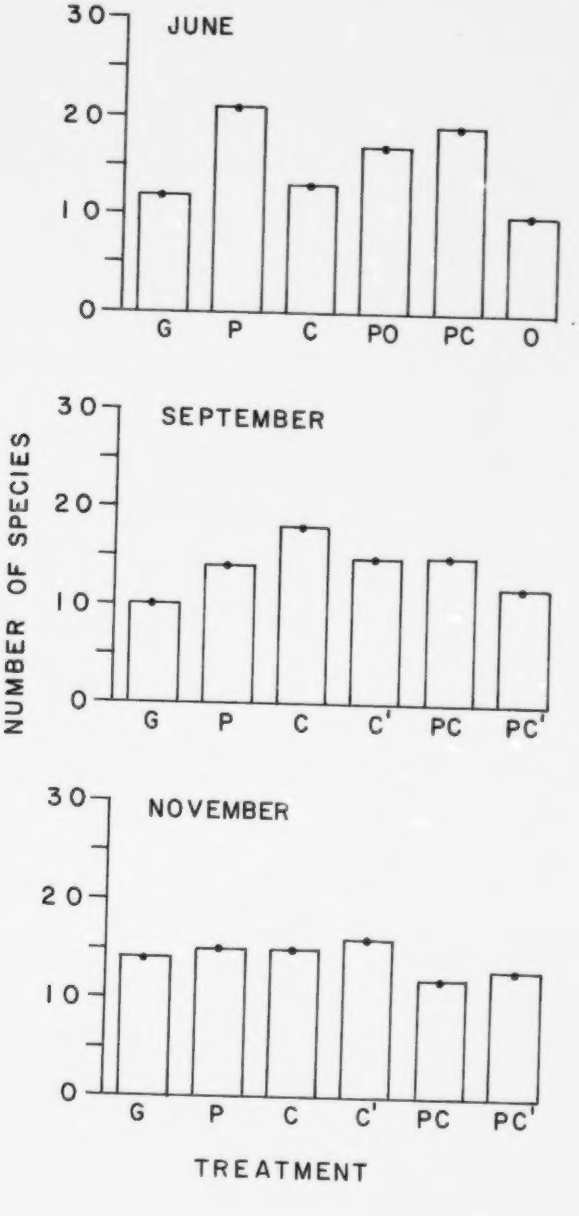

Fig. 6. Number of epifaunal species per sample for each treatment and control during the three sampling periods. Treatment designations are as follows: G=grass control; P=pen; C=cage; PO=pen + open cage; PC=pen + cage; O=open, topless cage; C'=new cage set; PC'=new cage + pen set.

had slightly more species than the open cage (O) and control (G). In contrast to species number the open cage treatment had more individuals/g of grass while the cage (C) and pen + cage (PC) had the least number of individuals/g grass (Fig. 7). These differences are primarily attributed to the differences in the density of the barnacle, Balanus improvisus (Table 8) which was very abundant in the open cage. Seven of the top ten dominant species were shared among all treatments including the control while Balanus was the dominant species and Crepidula the second or third most abundant species in each treatment. The top three species in each treatment constituted 90% or greater of all individuals recorded for each sample. This overwhelming dominance by a few species was the cause for the overall low H' (diversity) for the treatments in June (Fig. 8). There were also no major differences in H' among the treatments for June.

In September, all treatments had more species per sample than the control (Fig. 6) with the cage (C) treatment having the greatest number. Except for the cage treatment, the grass control, pen and pen + cage had fewer species than that recorded for June. The new cage (C') and new cage + pen (PC') had slightly fewer species than the comparable older treatments. This situation paralleled the response of the infauna to the new cage sets also for the September sampling data.

The density of epifaunal individuals per gram of grass in September was much greater in all treatments when compared to the control (Fig. 7). The highest density was found in the new cage (C') and pen + new cage (PC'). These very high densities were caused by the large numbers of Crepidula, which in five of the six treatments made up 98% or greater of the total epifauna (Table 9). Balanus and the isopod Erichsonella were either the second and third species in all the treatments. Dense concentrations of Crepidula were observed covering the blade from the tip to the base especially in the new cage treatment, but were not evident anywhere outside the experimental area in as dense concentrations. In addition, compared to June when seven of the ten species were found in all treatments, only four of the top ten were not found in all treatments.

The very low diversities of this sampling period, which were lower than those calculated in June, were a result of the overwhelming dominance by Crepidula. The slightly higher diversity value for the cage (C) treatment was due to the fact that Crepidula comprised only 90% of the total sample compared with 98% or greater in the other treatments.

By November, there appeared to be no difference in the total number of species in each sample (Fig. 6). However, there were large differences in the number of individuals among the different treatments (Fig. 7). The lowest density was found in the cage (C) and pen + cage (PC) treatments. This low density of individuals was due primarily to the fact that the abundance of grass in these older cages was very low. The oyster set that had occurred in these two

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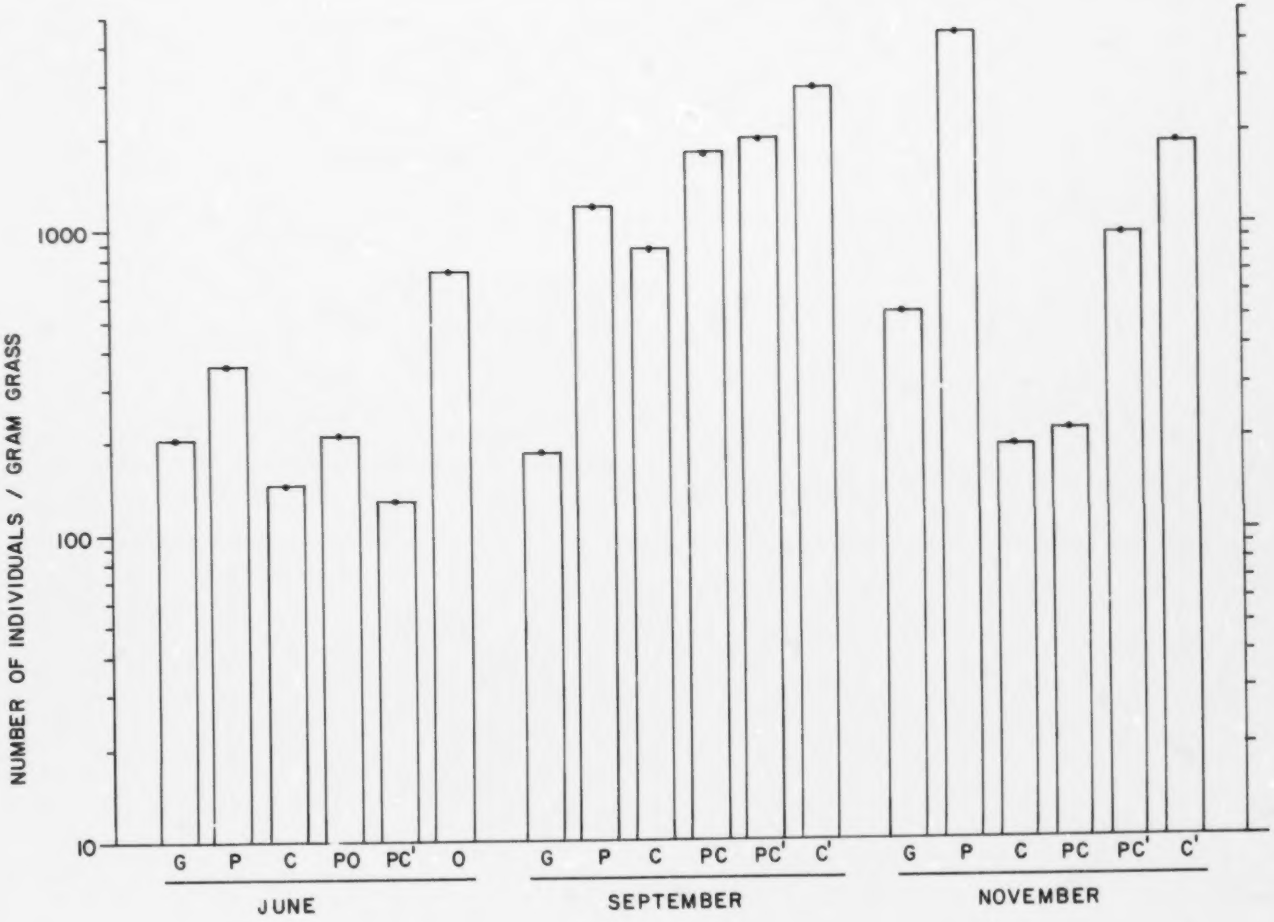

Fig. 7. Number of individuals per gram of grass for each treatment and control during the three sampling periods. Treatment designations are as follows: G=grass control; P=pen; C=cage; PO=pen + open cage; PC=pen + cage; O=open, topless cage; C'=new cage set; PC'=new cage + pen set.

TABLE 8. LIST OF THE TOP TEN DOMINANT SPECIES RECORDED FROM THE EPIFAUNAL CAGING EXPERIMENTS FOR JUNE. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE, ITS DENSITY PER GRAM OF GRASS, AND DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

MIXED

Species	$^o/_o$	dens/gm	dens/m^2
1. *Balanus improvisus*	86.61	180.05	20165.20
2. *Crepidula convexa*	4.69	9.74	1091.42
3. *Gammarus mucronatus*	2.23	4.64	519.72
4. *Erichsonella attenuata*	2.01	4.18	467.75
5. *Polydora ligni*	1.79	3.71	415.78
6. *Stylochus ellipticus*	0.78	1.62	181.90
7. *Nereis succinea*	0.45	0.93	103.94
8. *Astyris lunata*	0.45	0.93	103.94
9. *Ampithoe longimana*	0.33	0.70	77.96
10. *Nassarius obsoletus*	0.33	0.70	77.96
Totals	99.67	207.20	23205.57
Total sample	100.00	207.90	23283.54

CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. *Balanus improvisus*	79.80	118.48	13270.01
2. *Crepidula convexa*	6.68	9.91	1110.40
3. *Polydora ligni*	6.35	9.42	1055.57
4. *Bittium varium*	4.29	6.36	712.85
5. *Erichsonella attenuata*	0.82	1.22	137.09
6. *Nereis succinea*	0.66	0.98	109.67
7. *Stylochus ellipticus*	0.41	0.61	68.54
8. *Gammarus mucronatus*	0.41	0.61	68.54
9. *Cymadusa compta*	0.25	0.37	41.13
10. *Astyris lunata*	0.08	0.12	13.71
Totals	99.75	148.08	16587.51
Total sample	100.00	148.44	16628.64

PEN + CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. *Balanus improvisus*	81.46	105.17	11779.03
2, *Crepidula convexa*	7.49	9.68	1083.60
3. *Polydora ligni*	4.98	6.43	719.65
4. *Stylochus ellipticus*	1.32	1.70	190.25
5. *Erichsonella attenuata*	1.09	1.40	157.16
6. *Nereis succinea*	0.85	1.11	124.08
7. *Gammarus mucronatus*	0.74	0.96	107.53
8. *Bittium varium*	0.57	0.74	82.72
9. *Astyris lunata*	0.34	0.44	49.63
10. *Nassarius obsoletus*	0.34	0.44	49.63
Totals	99.19	128.07	14345.27
Total sample	100.00	129.0	14459.06

PEN + OPEN CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. *Balanus improvisus*	79.23	166.44	18641.61
2. *Erichsonella attenuata*	5.24	11.01	1232.75
3. *Crepidula convexa*	4.79	10.07	1127.52
4. *Polydora ligni*	3.51	7.38	326.85
5. *Gammarus mucronatus*	2.36	4.97	556.24
6. *Microprotopus raneyi*	1.02	2.15	240.54
7. *Nereis succinea*	0.96	2.01	225.50
8. *Cymadusa compta*	0.70	1.48	165.37
9. *Idotea baltica*	0.58	1.21	135.30
10. *Stylochus ellipticus*	0.51	1.07	120.27
Totals	98.90	207.79	23271.95
Total sample	100.00	210.05	23527.51

TABLE 8. CONTINUED.

OPEN CAGE					PEN			
Species	°/o	dens/gm	dens/m^2		Species	°/o	dens/gm	dens/m^2
1. *Balanus improvisus*	79.74	571.88	64050.00		1. *Balanus improvisus*	90.36	324.36	36328.20
2. *Crepidula convexa*	9.37	67.19	7525.00		2. *Erichsonella attenuata*	2.81	10.10	1130.77
3. *Stylochus ellipticus*	2.51	17.97	2012.50		3. *Crepidula convexa*	2.54	9.13	1023.08
4. *Bittium varium*	2.51	17.97	2012.50		4. *Bittium varium*	0.85	3.04	341.03
5. *Polydora ligni*	2.29	16.41	1837.50		5. *Stylochus ellipticus*	0.76	2.72	305.13
6. *Gammarus mucronatus*	1.42	10.16	1137.50		6. *Polydora ligni*	0.62	2.24	251.28
7. *Erichsonella attenuata*	1.31	9.38	1050.00		7. *Gammarus mucronatus*	0.49	1.76	197.44
8. *Nereis succinea*	0.44	3.13	350.00		8. *Nereis succinea*	0.40	1.44	161.54
9. *Astyris lunata*	0.33	2.34	262.50		9. *Caprella penantis*	0.27	0.96	107.69
10. *Cymadusa compta*	0.11	0.78	87.50		10. *Cymadusa compta*	0.22	0.80	89.74
Totals	100.00	717.18	80325.00		Totals	99.32	356.55	39935.90
					Total sample	100.00	358.95	40205.14

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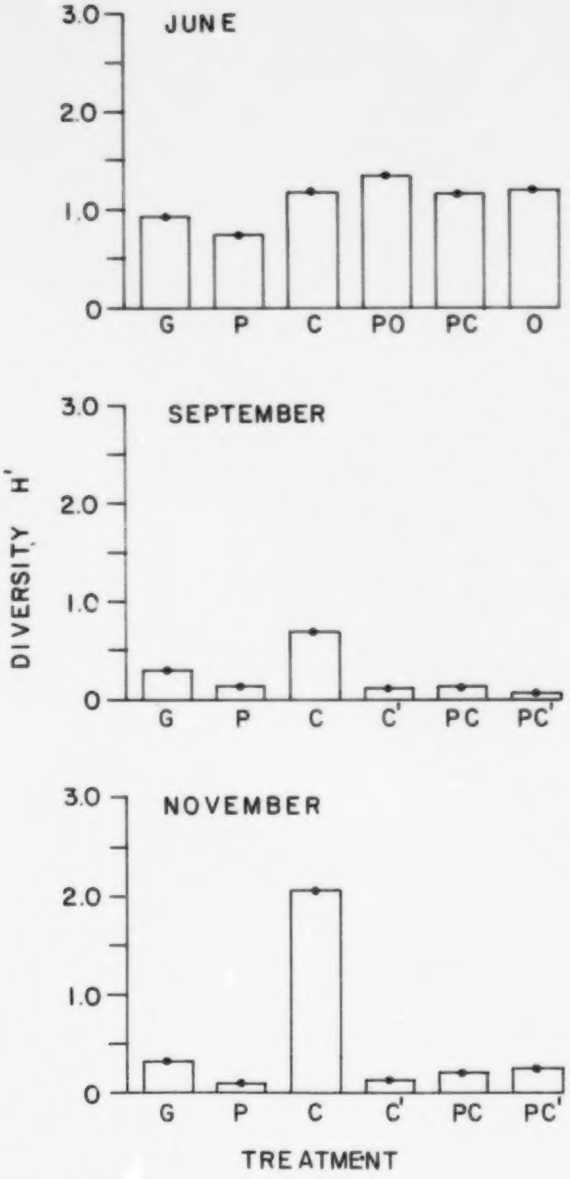

Fig. 8. Diversity values (H') for each treatment and control during the three sampling periods. Treatment designations are as follows: G=grass control; P=pen; C=cage; PO= pen + open cage; PC=pen + cage; O=open, topless cage; C'=new cage set; PC'=new cage + pen set.

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TABLE 9. LIST OF THE TOP TEN DOMINANT SPECIES RECORDED FROM THE EPIFAUNAL CAGING EXPERIMENTS FOR SEPTEMBER. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE, ITS DENSITY PER GRAM OF GRASS, AND DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

MIXED

Species	$^o/_o$	dens/gm	dens/m^2
1. Crepidula convexa	96.74	180.32	15868.56
2. Erichsonella attenuata	0.82	1.52	133.87
3. Balanus improvisus	0.54	1.01	89.25
4. Gastropoda	0.49	0.91	80.32
5. Nereis succinea	0.38	0.71	62.47
6. Idotea baltica	0.38	0.71	62.47
7. Paracaprella tenuis	0.33	0.61	53.55
8. Bittium varium	0.16	0.30	26.77
9. Ampithoe longimana	0.11	0.20	17.85
10. Anadara transversa	0.05	0.10	8.92
Totals	100.00	186.39	16404.03
Total sample	100.00	186.39	16404.03

CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. Crepidula convexa	90.09	772.53	67982.81
2. Balanus improvisus	3.39	28.76	2530.47
3. Erichsonella attenuata	2.40	20.39	1793.99
4. Ampithoe longimana	0.66	5.58	490.99
5. Astyris lunata	0.61	5.15	453.22
6. Nereis succinea	0.56	4.72	415.45
7. Doridella obscura	0.35	3.00	264.38
8. Cymadusa compta	0.33	2.79	245.49
9. Stylochus ellipticus	0.25	2.15	188.84
10. Bittium varium	0.13	1.07	94.42
Totals	99.66	846.14	74460.05
Total sample	100.00	849.13	74724.43

PEN + CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. Crepidula convexa	98.69	1746.04	153651.88
2. Balanus improvisus	0.49	8.72	767.55
3. Erichsonella attenuata	0.37	6.49	571.20
4. Bittium varium	0.15	2.64	232.05
5. Astyris lunata	0.11	2.03	178.50
6. Nereis succinea	0.03	0.61	53.55
7. Gastropoda	0.03	0.61	53.55
8. Cymadusa compta	0.02	0.41	35.70
9. Paracaprella tenuis	0.02	0.41	35.70
10. Stylochus ellipticus	0.01	0.20	17.85
Totals	99.92	1766.13	155597.53
Total sample	100.00	1769.16	155686.78

PEN +CAGE (NEW SET)

Species	$^o/_o$	dens/gm	dens/m^2
1. Crepidula convexa	99.45	1918.36	168815.38
2. Balanus improvisus	0.31	5.91	519.64
3. Erichsonella attenuata	0.11	2.18	192.04
4. Astyris lunata	0.04	0.44	67.78
5. Nereis succinea	0.02	0.39	33.89
6. Idotea baltica	0.02	0.39	33.89
7. Paracerceis caudata	0.01	0.26	22.59
8. Anthozoa	0.01	0.26	22.59
9. Stylochus ellipticus	0.01	0.13	11.30
10. Paracaprella tenuis	0.01	0.13	11.30
Totals	99.99	1928.78	169730.40
Total sample	100.00	1929.04	169753.00

TABLE 9. CONTINUED

CAGE (NEW SET)				PEN			
Species	$^o/_o$	dens/gm	dens/m^2	Species	$^o/_o$	dens/gm	dens/m^2
1. Crepidula convexa	98.89	2819.16	248085.94	1. Crepidula convexa	98.64	1165.12	102530.44
2. Balanus improvisus	0.29	8.13	715.24	2. Erichsonella attenuata	0.51	6.00	528.20
3. Erichsonella attenuata	0.24	6.82	600.29	3. Balanus improvisus	0.30	3.51	308.95
4. Ampithoe longimana	0.14	4.06	357.62	4. Nereis succinea	0.16	1.93	169.42
5. Astyris lunata	0.14	3.92	344.85	5. Ampithoe longimana	0.09	1.02	89.69
6. Cymadusa compta	0.13	3.63	319.30	6. Cymadusa compta	0.07	0.79	69.76
7. Nereis succinea	0.06	1.60	140.49	7. Stylochus ellipticus	0.06	0.68	59.80
8. Gastropoda	0.03	0.87	76.63	8. Gastropoda	0.06	0.68	59.80
9. Stylochus ellipticus	0.03	0.73	63.86	9. Bittium varium	0.04	0.45	39.86
10. Doridella obscura	0.02	0.58	51.09	10. Edotea triloba	0.02	0.23	19.93
Totals	99.97	2849.50	250755.31	Totals	99.95	1180.32	103875.85
Total sample	100.00	2850.82	250870.25	Total sample	100.00	1181.21	103945.61

treatments probably caused some of this reduction as well as from the overall reduction of light from the netting of the cages. The reduction in the density of the grass in the newer cages was not as dramatic since these cages were in the field for a shorter length of time. The pen had the highest density of epifauna where the grass density inside the pen was apparently not impacted by the presence of the pen.

Crepidula maintained the dominant ranking in all treatments through November (Table 10). The very large numbers in the pen (P) treatment caused the large numerical density for this treatment discussed above. In addition, *Crepidula* densities in all treatments except the cage (C) made up greater than 96% of the total sample. In the cage treatment where grass density was low, *Crepidula* made up only 49% of the sample.

Also in the November samples, only three species were shared dominants in all treatments compared with seven in June and four in September.

The diversity (H') of each treatment was very low again except in the old cage (C) because of overwhelming dominance by *Crepidula* in these treatments (Fig. 8). The decreased abundance of *Crepidula* in the old cage (Table 10) allowed the other species to assume a greater rank which resulted in a higher equilability component of H' for the cage treatment.

III. Blue Crab Stomach Analysis

The mastictory mode of feeding made the identification of gut contents to the species level difficult. Percent frequency of occurrence of food items indicated the blue crabs feed on both epifaunal and infaunal species (Fig. 9). *Zostera* was found in 70% of the stomachs analyzed. Generally, live, intact, and very uniformly cut sections of leaf material were present, indicating that crabs may ingest the blades but digest only the encrusting organisms. Epifaunal molluscs, isopods and *Balanus improvisus* were among the major food items in crab stomachs. *Callinectes* also foraged among the rhizome mat on infaunal molluscs. Feeding burrows and infaunal feeding were frequently observed in the field.

IV. Sediments

Table 11 presents the percent sand, silt and clay in the sediments taken from the various treatments in the sand and grass habitats in November, 1969. Within the sand habitat and grass habitat, there appeared to be little difference among the treatments. The percent sand in the grass control (G) and new cage (C') was not different from the sand. However the percent silt was higher in these same grass treatments compared to the sand.

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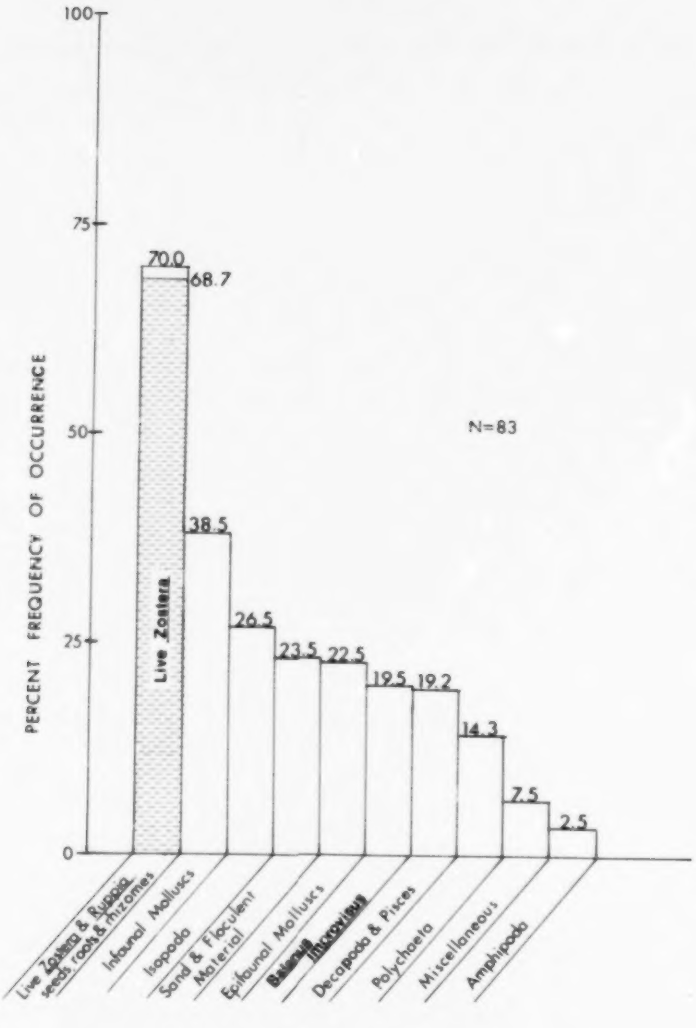

Fig. 9. Percent frequency of occurrence of food items in Callinectes sapidus stomachs.

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TABLE 10. LIST OF THE TOP TEN DOMINANT SPECIES RECORDED FROM THE EPIFAUNAL CAGING EXPERIMENTS FOR NOVEMBER. NUMBERS REPRESENT PER CENT COMPOSITION THAT EACH SPECIES COMPRISES OF THE TOTAL SAMPLE, ITS DENSITY PER GRAM OF GRASS, AND DENSITY PER M^2. TOTALS FOR THE TOP TEN AND FOR THE TOTAL SAMPLE ARE ALSO GIVEN.

MIXED

Species	$^o/_o$	dens/gm	dens/m^2
1. *Crepidula convexa*	96.13	506.42	51401.82
2. *Erichsonella attenuata*	1.74	9.17	931.19
3. *Balanus improvisus*	1.18	6.19	628.55
4. *Polydora ligni*	0.26	1.38	139.68
5. *Gastropoda*	0.20	1.03	104.76
6. *Doridella obscura*	0.17	0.92	93.12
7. *Idotea balthica*	0.13	0.69	69.84
8. *Nereis succinea*	0.04	0.23	23.28
9. *Bittium varium*	0.04	0.23	23.28
10. *Stylochus ellipticus*	0.02	0.11	11.64
Totals	99.91	526.37	53427.16
Total sample	100.00	526.81	53473.72

CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. *Crepidula convexa*	49.21	94.46	9587.67
2. *Paracaprella tenuis*	27.13	52.08	5285.87
3. *Cymadusa compta*	11.98	22.97	2333.66
4. *Ampithoe longimana*	4.18	8.03	815.37
5. *Balanus improvisus*	2.31	4.43	449.86
6. *Melita appendiculata*	1.15	2.22	224.93
7. *Caprella penantis*	1.01	1.94	196.81
8. *Polydora ligni*	0.87	1.66	168.70
9. *Erichsonella attenuata*	0.58	1.11	112.47
10. *Melita nitida*	0.43	0.83	84.35
Totals	98.85	189.75	19259.69
Total sample	100.00	191.96	19484.62

PEN + CAGE

Species	$^o/_o$	dens/gm	dens/m^2
1. *Crepidula convexa*	97.86	212.34	21552.75
2. *Balanus improvisus*	0.67	1.46	148.18
3. *Erichsonella attenuata*	0.55	1.19	121.23
4. *Cymadusa compta*	0.55	1.19	121.23
5. *Doridella obscura*	0.09	0.20	20.21
6. *Paracaprella tenuis*	0.09	0.20	20.21
7. *Stylochus ellipticus*	0.03	0.07	6.74
8. *Nereis succinea*	0.03	0.07	6.74
9. *Polydora ligni*	0.03	0.07	6.74
10. *Idotea baltica*	0.03	0.07	6.74
Totals	99.93	216.86	22010.77
Total sample	100.00	217.00	22024.25

PEN + CAGE (NEW SET)

Species	$^o/_o$	dens/gm	dens/m^2
1. *Crepidula convexa*	97.23	915.42	92915.38
2. *Balanus improvisus*	1.35	12.69	1287.69
3. *Erichsonella attenuata*	0.61	5.72	580.72
4. *Doridella obscura*	0.26	2.49	252.49
5. *Cymadusa compta*	0.21	1.99	201.99
6. *Anadara transversa*	0.08	0.75	75.75
7. *Stylochus ellipticus*	0.05	0.50	50.50
8. *Gammarus mucronatus*	0.05	0.50	50.50
9. *Caprella penantis*	0.05	0.50	50.50
10. *Nereis succinea*	0.03	0.25	25.25
Totals	99.92	940.81	95490.77
Total sample	100.00	941.56	95566.52

TABLE 10. CONTINUED.

CAGE (NEW SET) Species	°/o	dens/gm	dens/m^2	PEN Species	°/o	dens/gm	dens/m^2
1. *Crepidula convexa*	98.92	1563.47	158692.25	1. *Crepidula convexa*	99.22	4274.45	433856.56
2. *Balanus improvisus*	0.32	5.02	509.82	2. *Erichsonella attenuata*	0.27	11.68	1185.40
3. *Erichsonella attenuata*	0.26	4.11	417.12	3. *Doridella obscura*	0.11	4.74	481.57
4. *Astyris lunata*	0.25	3.88	393.95	4. *Balanus improvisus*	0.08	3.65	370.44
5. *Doridella obscura*	0.04	0.68	69.52	5. *Gastropoda*	0.05	2.19	222.26
6. *Cymadusa compta*	0.04	0.68	69.52	6. *Cymadusa compta*	0.04	1.82	185.22
7. *Polydora ligni*	0.03	0.46	46.35	7. *Paracaprella tenuis*	0.04	1.82	185.22
8. *Oxyurostylis smithi*	0.03	0.46	46.35	8. *Nereis succinea*	0.03	1.46	148.18
9. *Gastropoda*	0.01	0.23	23.17	9. *Bittium varium*	0.03	1.46	148.18
10. *Ampithoe longimana*	0.01	0.23	23.17	10. *Idotea baltica*	0.03	1.46	148.18
Total	99.91	1579.22	160291.22	Total	99.90	4304.73	436931.21
Total sample	100.00	1580.60	160430.24	Total sample	100.00	4307.90	437264.60

TABLE 11. PERCENT SAND, SILT AND CLAY IN THE SEDIMENTS TAKEN FROM THE DIFFERENT SAND AND GRASS TREATMENTS IN NOVEMBER, 1979 (NUMBERS REPRESENT MEANS OF THREE SAMPLES).

TREATMENT	SAND	CLAY	SILT
Sand (control)	94.2	4.7	1.1
Sand + Cage	93.6	5.5	0.9
Sand + Pen	Samples Lost		
Sand + Pen + Cage	93.6	5.5	0.9
Grass (Control)	92.2	5.2	2.6
Grass + Cage (old)	88.7	7.9	3.4
Grass + Cage (new)	92.9	4.9	2.2
Grass + Pen	90.2	6.3	3.5
Grass + Pen + Cage (old)	90.2	6.5	3.3
Grass + Pen + Cage (new)	90.4	6.2	3.5

The cage and pen treatments in the grass (except the new cage) had less sand and more clay and silt than the control plot. The old cage had the lowest percentage of sand and the highest percentage of clay, a result of this cage being out the longest. These alterations in the sediment fractions are not of a large magnitude. This may be because the treatments were not in the field for a long enough time to create sediment alterations and that the very dynamic nature of this area prevents fine sands and silts and clays from accreting. It may also indicate that the cages and pens did not have as significant impact on the sediments as originally hypothesized.

DISCUSSION

Benthic environments colonized by submerged vegetation represent a unique habitat with respect to their impact on the associated faunal communities. The most notable characteristic of these beds are the large densities of animals that are found associated with SAV compared to the surrounding, unvegetated sediments (Thayer et al., 1975; Orth 1977; Reise, 1977b; Orth and Heck 1980; Heck and Orth 1980a). Recent interest has centered on the factors that cause such high densities (e.g. increased physical heterogeneity, decreased predation rates and increased food) (Orth 1977; Reise 1977a; Peterson 1980; Nelson 1979; Stoner 1980; Heck and Orth 1980b).

The advent of manipulative techniques in understanding function as well as structure of the benthic community has clearly identified major factors that overwhelmingly influenced the makeup of the community (Virnstein, 1977; Woodin 1974; Young et al. 1976; Reise 1977 a,b; Orth 1977; Peterson 1980). Though there are distinct problems in field manipulation experiments, especially predator exclusion cages (Virnstein 1978; Peterson 1980), these manipulative techniques have been extremely useful in allowing a more thorough examination of causative factors through experimentation, rather than previously stressed correlative information.

Despite some of the difficulties encountered in the caging and pen experiments (e.g. the breaching of the pen in June just prior to our sampling and the crab disturbance of the sand cages), our results suggest that exclusion of predators through cages and pens has an impact on the macroinvertebrate fauna inhabiting the sand and grass habitats.

Several trends were evident over the entire sampling period. With respect to numbers of species, the grass habitat always had more infaunal species per core than the sand habitat for all treatments. There were apparently no distinct differences among the grass treatments for species infaunal numbers but in the sand, species numbers were higher in pen and cage treatments compared with the control, with the cage treatments (C and PC) in June having the most dramatic effect on increased numbers of species. However, once the cages were disturbed and new ones set to replace the disturbed ones, the effects were not as dramatic though species numbers were stil higher compared to the control.

In addition, except for the sand cage treatments (C and PC) in June, there appeared to be no difference between the pen and cage treatments for numbers of species in both habitats.

Infaunal species numbers were lower in September compared to June and November. This could possibly be a result of natural mortality due to high summer time water temperatures as well as predation activity in the uncaged and unpenned areas, and also possible predatory activities of infaunal species on other infaunal species that could not be detected through our study design. Similar summer time depressions in infauna were observed by Virnstein (1977) for the York River, Virginia.

Density of individuals in the grass habitat treatments was generally higher than the sand habitat treatments except for the June cage treatments. The differences in densities were not as pronounced in the September period as in the other two periods. The September density in the grass control this month was very similar to the sand treatments, but by November, the differences in densities had increased between the sand and grass habitats.

In the sand area, densities were always higher in the cage and pen treatments compared to the control in all months while in the grass habitat only the September treatment densities were higher than the control.

As with the species number, densities of infauna decreased in the summer both in the sand and grass habitat. The large depressions in the grass control suggests that predation in grass habitats can be significant, especially in the summer when not only crabs are present but also different benthic fish predators. The difference between the higher numbers persisting in the treatments versus the control for September's grass infauna possibly relates to that portion of the infauna that escapes predation via the cages or pens.

The grass habitat acts as a refugia for infauna though many individuals are still cropped by predatory effects during the period when predation may be intense (e.g. summer periods). It is interesting to note that the decrease in infaunal densities from June to September was similar for both the sand (19%) and grass habitat (17%). Those grass infauna surviving the high summer predation levels do so primarily because of the presence of the grass.

Species numbers and density in the new cages in the grass area were lower than comparable figures for the older cages. This suggests that timing of the placement of cages has an effect on the settlement densities as recruitment periods for different species may vary, exposing the benthic environment to a different suite of recruits at different periods.

Species response to the cages and pens in the sand and grass habitats was variable. Gemma gemma, a sand dominant, persisted in the cage and pen areas, but was almost entirely eliminated from the sand control area by predation, either by blue crabs or rays which frequented this habitat all summer. The large increase in Mya in the June cage areas in the sand only suggests a cage effect in that the reduction in current velocity inside the cages may have allowed high densities of Mya to settle preferentially. It is also possible that the planktonic larvae of Mya, when contacting the cage surface, initially attached to the cage via byssal threads and then fell into the cage as they got older, which could explain why they were not as dense in the pen treatment (P). The absence of Mya in the grass habitat cages cannot be explained except by vagaries of planktonic recruitment or the grass bed acting as a filter and allowing a more even settlement of Mya throughout the grass area.

Crassostrea, the American oyster, appeared to be affected by the older grass cages. Like Mya it has planktonic larvae and the conditions that favored Mya settlement may have been the same for the oyster. Crassostrea attached to the blades of grass and subsequently grew on the bottom. The lack of a hard substrate in the sand cages (oysters do not produce byssal threads) may be the reason for lack of oyster settlement in the bare sand area.

The results of our caging work present both similarities and dissimilarities to recent work done in other comparable grass habitats. Reise's (1978) data paralleled our results where predator exclusion experiments he conducted had greater impact in unvegetated habitats than vegetated habitats, which was similar to what we found in our experiments. Reise concluded that predation was mitigated by the spatial resistance of the grass and limited accessibility. Orth (1977) showed densities in caged treatments significantly increasing over short periods of time in similar vegetated habitats in the Chesapeake Bay. The cause for this difference may be timing at which cages were initialized, i.e. August in Orth's study and April and June in this study. This suggests that the timing of the cage placement relative to predatory activities may be critical in understanding the role of predation in these habitat.

Epifauna densities were impacted by the cage's effect on the growth of grass inside the cage. This was particularly evident in the older cages where, compounded with the dense set of oysters and fouling on the cages, the density of grass was reduced inside the cages compared to outside the cages. In discounting the cages and their effect on the grass density, the pens alone, where grass density was not affected, had a large effect on epifaunal densities. In June, densities of Balanus were higher in the pen treatment and in September and November, the very high densities of Crepidula inside the pen were responsible for the large differences inside and outside the pen. In September the new cages (C' and PC'), which had not drastically affected the growth of grass, also had very high densities of Crepidula. Some stomachs of blue crabs examined during this period

(1979) which had different contents than those examined in 1978, suggest that blue crabs were feeding on *Crepidula* and that their exclusion from the penned area and newer cages caused the high densities of *Crepidula* to persist. Blue crabs do ingest grass and most likely whatever is on the blades. Being very opportunistic they will feed on anything that is available. The large abundance of food, both in the sediment and on the blades, allow the blue crab an ample food supply.

It appears that during the course of this experiment, predators (including fish) consumed large quantities of food items from the sediments and grass. The large secondary production estimates observed from additional work done in this area (see Section IV on Secondary Production) suggest an enormous food supply available for consumption by many predator species, both fish and invertebrates. Our data show large reductions of both epifauna and infauna between June and September in open, uncaged or unpenned areas and that the presence of the pens or cages had a significant impact on the survivalship of prey species. The results here support many of the recent works cited above on the importance of predation in structuring the benthic fauna and that this fauna provides a significant supply of food to those predators.

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CHAPTER 3

PREDATOR-PREY INTERACTIONS IN A ZOSTERA MARINA (EELGRASS) ECOSYSTEM IN THE LOWER CHESAPEAKE BAY, VIRGINIA

by

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and

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ABSTRACT

Experiments were conducted with artificial seagrass in small wading pools to assess the ability of prey to survive predation at different densities of grass. Experiments using *Mulinia laterialis*, a bivalve, as prey, and adult *Callinectes sapidus*, a crab, as predator, showed that almost no *M. lateralis* survived at 3 different densities of grass. Experiments with juvenile *C. sapidus* as prey and adult *C. sapidus* as predator showed greatest survival at highest densities of grass. The behavior of the juvenile crabs in relation to its predator was different in the presence of the grass than in its absence. It was believed that the survival of a particular prey species in a vegetated habitat will depend upon the life style and life cycle of both prey and predator and the density and morphology of the vegetation.

INTRODUCTION

A species presence or absence and its abundance in any particular habitat is regulated by its physiological tolerances, morphological constraints, habitat preferences, and biological interactions such as competition and predation with other animals (Dayton, 1971; Connell, 1972; Virnstein, 1977; Nelson, 1979a, b; Stoner, 1980a, b, c). Predation is a significant biological interaction in aquatic systems and has been shown to be the primary structuring agent in many recent ecological studies in terrestrial, freshwater and marine systems (Paine, 1966; Dayton, 1971; Brooks and Dodson, 1965; Connell, 1975). The ability of a prey species to avoid a predator will depend on the morphological and behavioral modifications that the prey has evolved over time in response to predation. In addition, the ability of the habitat to mediate the effect of predation can play a significant role in the survival of the prey (Stoner, 1980c).

Seagrass systems contain a very dense and diverse macroinvertebrate assemblage (Orth, 1973; Kikuchi and Peres, 1977) in which predation plays an important if not key role in structuring the associated faunal community (Nelson, 1979a, b; Heck and Orth, 1980a). Several studies have also alluded to the idea that vegetational density can have a significant affect on the survival of the prey (Weinstein and Heck, 1979; Heck and Orth, 1980a, b; Orth and Heck, 1980; Stoner, 1980b; Heck and Thoman, 1981). Our objectives in this study were to examine predator-prey interactions in a *Zostera marina* dominated system and to assess the prey's ability to survive predation at different vegetational densities.

MATERIALS AND METHODS

Two prey species with very different life styles were chosen for predation experiments. We used a sedentary infaunal bivalve, *Mulinia lateralis*, in one series of experiments. *Mulinia* is ubiquitous throughout the Bay and inhabits a variety of sediment types where it burrows to a depth of 2-3 cm. This species grows to a length of approximately 2.5 cm and undergoes periodic population eruptions, particularly in the spring (Boesch, 1973, 1974). However, the dense *Mulinia* populations experience high mortalities in the summer, most likely due to predation (Virnstein, 1977).

Juvenile blue crabs, *Callinectes sapidus*, were used as prey in the second set of experiments. *Callinectes* is highly motile and juveniles are characteristically abundant in vegetated habitats of the lower Bay (Heck, 1981). This species is very important commercially, being second only to oysters (*Crassostrea virginica*) in terms of dollars contributed to Virginia's seafood economy.

Large, adult male *C. sapidus* were used as predators in both sets of experiments. Blue crabs are voracious predators and can be considered a keystone species (sensu Paine, 1966) in structuring Chesapeake Bay benthic communities (Virnstein, 1977).

Prey refuge experiments were conducted in three wading pools (2.43 m diameter x 0.45 m high). Each pool had 10-13 cm of sand placed on the bottom and was filled with estuarine water from the York River. Predation experiments on *Mulinia* were conducted outdoors using a flow-through water system whereas those on *Callinectes* were set up indoors. Water from each indoor pool was continually pumped through a large header tank which contained crushed oyster shell to insure adequate oxygenation and removal of any suspended material (Fig. 1). Each pool in both sets of experiments received additional aeration from two piston air pumps.

Artificial *Zostera marina* rhizomes and leaves were used to simulate the live system. Three densities of rigid plastic netting (1 inch diameter) measuring 1 m x 1 m (Conwed Corp. Vexar) were used to simulate the rhizomes. High density mats were arbitrarily set at the normal plastic mesh density. Medium and low density mats were reduced proportionately by cutting out cross mesh strands.

Extruded polypropylene ribbon 5 mm wide and tinted green was used to simulate the leaves. Three densities of grass were chosen for the experimental treatments: a high density count consisting of 1600 blades/m^2; a medium density count consisting of 800 blades/m^2; and a low density count consisting of 400 blades/m^2. The high values were approximated from maximum stem density counts of eelgrass from a *Zostera marina* bed at the mouth of the York River, Virginia. Artificial grass was attached to the artificial rhizomes for those treatments testing both rhizome and leaf effects. This was done by taking a single strand 30 cm long and tying it in half around the plastic rhizome mat yielding 2 strands, each approximately 15 cm long. Low densities of grass blades were attached to low rhizome density mats, medium density blades to medium density rhizomes and high density blades to high density rhizomes based on the assumption that in *Z. marina* beds, there is a positive correlation between blade and rhizome densities. Biomass measurements from different *Z. marina* beds support this assumption (Orth and Moore, 1982). All rhizome mats (with or without leaves) were placed 1 to 2 cm beneath the sediment surface in each pool.

Adult male *Callinectes* were collected from a large *Zostera marina* bed at the mouth of the York River using an otter trawl and maintained in holding tanks. Prior to being used in experiments, all predators were starved for 48 hours by placing them in wire mesh cages, which prevented them from effectively foraging in the holding tank. Care was taken to handle the crabs as gently as possible to prevent damage to the crab. Only males ranging in size from 10 to 15 cm (carapace width), that had all appendages and no visible, external breaks in the exoskeleton were used. Any male that was near the shedding phase was not used.

The *Mulinia-Callinectes* experiments initially tested the effects of high density rhizome mats and also the high density rhizome and leaf combination on

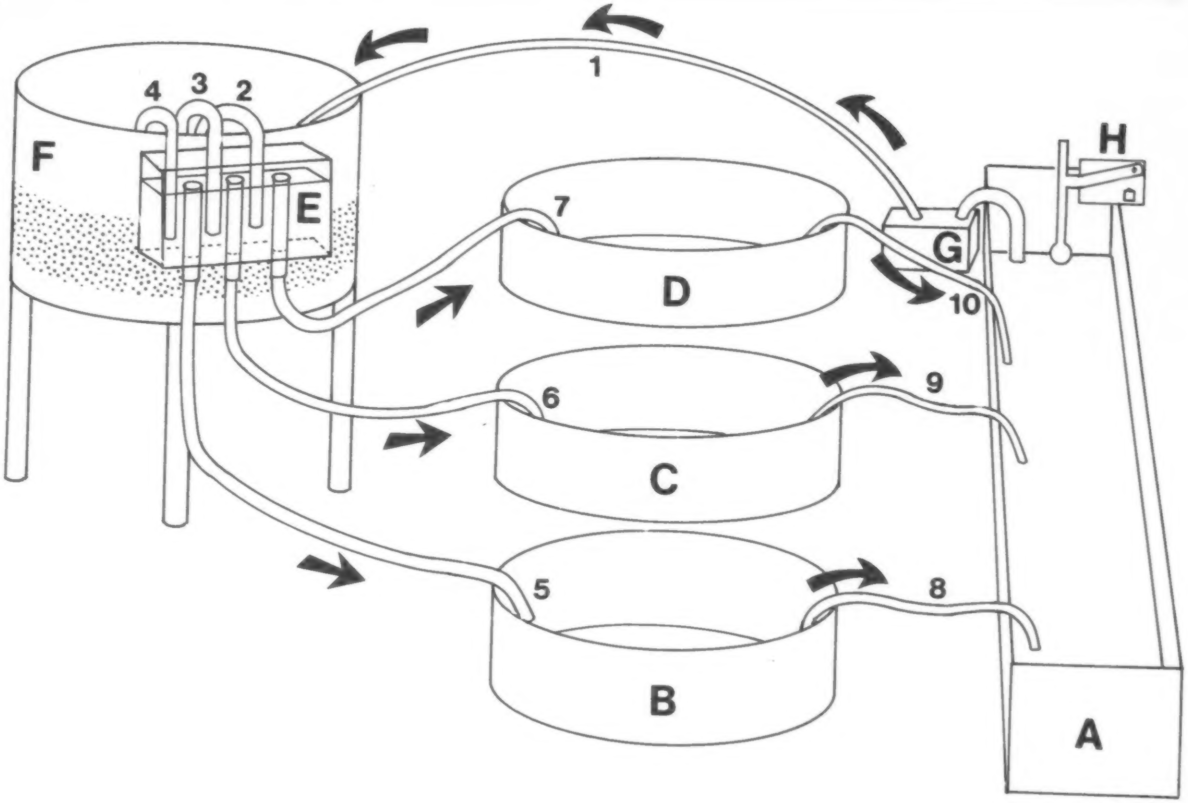

Fig. 1. Design of experimental pools used in predator-prey tests.

This system combines both gravity flow and pump driven circulation of water. Water from reservoir A is forced by Pump G into filter bed F. Due to the positioning of the pump below the water level in reservoir A, the pump is self priming and the electrical power for the pump is controlled by float switch H. Should the water level in reservoir A drop below a critical level, the switch will shut off power to the pump. Water from the pump enters filter bed F on top of a layer of crushed oyster shells. The water then travels down through the biologically active oyster shells until it reaches a dead water space at the bottom of the filter bed. Water is removed from this dead space by siphon lines 2, 3 and 4, and transferred to tank E. By raising or lowering tank E, the water level of the filter bed may be adjusted to the desired height. Three overflow pipes connected to hoses 5,6, and 7 distributes water to the three experimental pools B,C, and D. Water leaving the experimental pool travel via siphon lines 8,9 and 10 back to reservoir A.

the survival of Mulinia. This was done because we assumed that if the bivalves received little or no protection from the high density treatments, there would be no refuge at lower rhizome and grass densities. One pool with no artificial vegetation was also established and each treatment was randomly assigned to each pool. Mulinia were provided from laboratory cultured stocks grown at the VIMS Eastern Shore Laboratory. One hundred Mulinia ranging in size from 1.5 to 2.5 cm were placed within the boundaries of each mat or within a 1 m^2 area at the center of the pool with no artificial vegetation. Prior to introducing the predators the Mulinia were left undisturbed from 24 to 48 hrs until all individuals had burrowed into the sediment. Two predators per pool were then introduced between 0800 and 1000 hrs and experiments were terminated 24 hrs later. The crabs were removed from each pool and the remaining Mulinia were enumerated after raking and sieving the sediment.

The initial Callinectes-Callinectes experiment tested the condition thought to provide the greatest and least protection, respectively, to juvenile crabs: high density leaves/rhizomes in one pool and no leaves/rhizomes in a second pool. It was again assumed that if no refuge existed for juvenile Callinectes at high density leaves/rhizomes, there would be no refuge at lower densities. Since the prey appeared to derive some protection from the high density treatment (see results), medium and low density treatments were also tested. Experiments were conducted simultaneously in pools with sand but without artificial grass mats. Treatments were randomly selected and assigned to each of the 3 pools. Only combinations of rhizome mats and grass were used because it was assumed that juvenile crabs, being motile prey, would not remain buried when approached by a crawling predator, and therefore the rhizome mat alone would provide little or no protection. Leaves provide the greatest protection for juvenile crabs by restricting the visual cues initiating predator attack and by presenting a physical barrier to successful predation encounters.

Juvenile male and female blue crabs ranging in size from 4 to 6 cm in carapace width were separated from otter trawl collections taken in a York River Zostera marina bed and held in a flow-through tank for use as prey. Only intact crabs showing no signs of molting were used. Ten prey were placed in each of three pools and left to acclimate for 24 hrs. Four predators were then introduced into each pool. Experiments were terminated 48 hrs later and all remaining crabs were removed, measured and examined for any physical damage.

Salinity and both sediment and water temperature were monitored twice during each experiment. Frequent visual observations were made of predator and prey behavior in each pool from a vantage point that caused minimal disturbance to the experimental animals. All experiments were conducted under ambient light conditions.

RESULTS

Mulinia-Callinectes Experiments

Data from two complete experimental series (Table 1) indicate that Mulinia received virtually no protection from either the high density rhizome

TABLE 1. NUMBER OF *MULINIA* SURVIVING IN 24 HOUR EXPOSURES TO *CALLINECTES* AT HIGH RHIZOME DENSITY, HIGH LEAF/RHIZOMES DENSITY AND BARE SAND (EACH TREATMENT UTILIZED 100 *MULINIA* and 2 *CALLINECTES*).

	Percent *Mulinia* Surviving	
Treatment	Test 1	Test 2
High Leaf/Rhizome	2	1
High Rhizome	2	1
Bare Sand	2	3

TABLE 2. NUMBER OF JUVENILE *CALLINECTES* SURVIVING IN 48 HOUR EXPOSURES TO ADULT *CALLINECTES* AT THE DIFFERENT LEAF/RHIZOME DENSITIES.

Treatment	Percent of juvenile *Callinectes* surviving - Test No.									
	1	2	3	4	5	6	7	8	9	$\bar{x}$
High	70	70		80	70	60	100			77
Medium			80					100	100	93
Low	50	20	60	60	40	90	70		80	59
None	30	20	30	50	30	0	30	0	40	26

component or a combination of high density leaves and rhizomes.

Our observations indicated that Callinectes began feeding on Mulinia soon after they were introduced into the pools regardless of the experimental treatment being tested.

Callinectes-Callinectes Experiments

The initial test conducted with three adult predators and 10 juvenile prey in each pool yielded 90% survival in the pool with high density rhizomes and leaves and only 20% surviving in sand. This suggested a protective value of grass for juvenile Callinectes. We then proceeded to test the effects of other vegetational densities on prey survival.

Nine experiments were conducted at four different levels of leaf density (high, medium, low and none) (Table 2). Only three tests were run with the medium grass density because of inadequate time and the reduced availability of suitably sized crabs. Declining water temperatures caused the adult male crabs to move into deeper water while most individuals of the year class that provided the prey had grown too large. Lower water temperatures also caused crabs in several later experiments to be lethargic thus confusing interpretations of vegetational refuge effects. These data were not included here.

Several earlier tests were aborted because the water flow was interrupted due to pump breakdowns causing conditions in the pools to change. Crabs behaved differently in these situations, being more lethargic. Thus the number of replicate experiments was lower than that originally planned.

Experimental data were statistically treated using a one way analysis of variance and the Student-Newman-Keuls multiple comparison test for unequal sample size was used for testing differences among the means (Table 2). Because of the nature of the data (counts), they were square root transformed $\sqrt{(x + .5)}$ and then the calculations were performed. There was a significant difference ($p<.01$) between the vegetated and the unvegetated treatments. However, there was no significant difference among the three densities of vegetation though the trend in the means indicated that low density vegetation had less of a refuge value than the high and medium dense vegetation. We feel that increased replicability could have reduced the variability but environmental considerations (low temperatures) did not allow for further effective experimentation.

Observations on both juvenile and adult Callinectes during the course of the experiments provided some insight into predator-prey behavior as affected by the presence or absence of vegetation. When first placed in the pools with no vegetation, juvenile C. sapidus initially moved around the entire pool and eventually burrowed randomly throughout the pool. However, when placed in the pools with vegetation, juveniles initially exhibited the same random movement but then virtually all individuals gravitated towards the grass mat and burrowed within its boundaries.

When predators were introduced after the juveniles had acclimated to the pools for 24 hours, different responses were again elicited by the juveniles depending upon the presence or absence of the artificial vegetation. The introduction of predators into the unvegetated pools caused the juveniles to immediately emerge from the sand and move actively around the pool in an attempt to avoid predation. In several experimental replicates without vegetation, a juvenile would be caught and either be eaten or lose several limbs soon after the introduction of the predators. The restless disposition of the prey in these treatments was evident during the entire experiment. In contrast, when the adult crabs were introduced into the vegetated pools, juveniles remained buried or hidden in the grass plot for the duration of the experiment. This was particularly true in treatments with highest density vegetation.

The adult crabs behaved in a dissimilar manner at the three different densities of vegetation. At the high density vegetation, they were rarely seen foraging inside the vegetation zone although some were occasionally observed resting on the artificial blades. It appeared that the dense area of blades impeded their ability to forage effectively. Adult crabs were frequently observed in the low density vegetated area and their movements did not appear to be as significantly impeded by the grass as they were in the densely vegetated plot. Remains of juvenile crabs were seen in the sparse vegetation but where these prey were actually caught was not witnessed.

DISCUSSION

Beds of submerged aquatic vegetation serve as both a refuge from predation and a feeding area. Though a species might utilize a grassbed for multiple reasons (e.g. both feeding and protection), it is important to separate the relative ecological role of each. Furthermore, a species utilization of a grassbed may vary depending on its life cycle stage. For example the habitat may be more important as a refuge to a juvenile individual of a species but may shift towards importance as a feeding area in the adult stage. Or efforts concentrated on examining the refuge function of eelgrass.

The results of our experiments suggest that beds of submerged vegetation do not have the same refuge value for all species. Mulinia received little protection from the presence of the vegetation. Its only escape responses is to retract into its thin shell. Even in very dense vegetation, a predator, such as the blue crab, has easy access to Mulinia which helps to explain why this species is never very abundant in vegetated habitats. Mulinia undergoes population eruptions but numbers are rapidly reduced by predators. Only in those situations where they have been completely protected from predators (e.g. inside predator exclusion cages) do large numbers of Mulinia survive for a significant length of time (Virnstein 1977; our unpublished data from the pen experiments for this project).

Juvenile Callinectes, on the other hand, were significantly protected by the vegetation and the degree of protection appeared to be related to vegetational density. Submerged plants visually and physically impede a predator thereby interfering with its search attack strategy. It was probably for this reason that the juveniles we observed remained within the artificial grass mat when a predator approached.

Our experiments involved only one predator and two prey species. However, when our results are considered with both those of Ken Heck of the Philadelphia Academy of Natural Sciences (unpublished) who conducted similar experiments and with other previously published accounts of predator-prey interactions (Heck, 1981; Heck and Thoman, 1981) a more generalized scheme of such relationships in grassbeds can be conceptualized. The following scheme incorporates the importance of predator and prey life styles, life cycle stages, and the density and morphology of the vegetation.

1. In general, vegetated habitats provide a greater refuge for mobile prey than for more sedentary prey. Among the mobile epifaunal species, those that are highly motile (e.g. juvenile fish, shrimps, and crabs) will be less susceptible to predation than those which are slower moving (i.e. isopods and amphipods) in a three dimensional habitat (grassbed) than in a two dimensional habitat (bare sand). This is particularly true if the predator has a search and destroy type strategy rather than an ambush type approach. Among the sedentary infaunal prey species, the refuge value of the grassbed will not differ greatly from that of a bare sand habitat. Instead it will depend on the lifestyle and biology of the prey rather than as much on the presence of the grass. The degree of protection for such species will depend on whether or not it is a tube dweller, if it has some external means of protection such as a shell and if so, the nature and quality of the shell, and lastly, the vertical extent to which the species can burrow. Sedentary infaunal species that build tubes will recieve greater protection than non-tube builders in both kinds of habitats. However, species which are able to burrow beneath the rhizome layer will derive more protection than those which burrow equally as deep in unvegetated areas. In addition, species that live in tubes that extend well below the sediment surface receive adequate protection from the rhizome mat so that their abundances are not greatly affected by additional protection from predators (e.g. via predator exclusion cages). These facts have been demonstrated for the deep burrowing polychaetes such as *Heteromastus filiformis* and *Spiochaetopterus oculatus* (Orth 1975, 1977; Virnstein, 1977) which were more abundant in vegetated areas than adajcent non-vegetated areas and also which were equally abundant inside and outside predator exclusion cages in the two respective areas. The refuge value for tubeless sedentary forms will also depend on their position in the sediment horizon with those species living closer to the sediment surface being more susceptible to predation. Our data show this to be true for *Mulinia* which lives just below the sediment surface and which derives virtually no protection from its thin shell against blue crab predation. Within a grassbed, epifaunal tube builders would be less protected than those which are infaunal since the latter could be protected by rhizome layer. Yet we hypothesize that epifaunal tube builders have a greater chance of survival than epifaunal non-tube builders.

2. The refuge value of the vegetation will invariably be a function of the different stages of the life cycle of a species. For example, a juvenile blue crab is highly protected by the vegetation. However, once the crab reaches a certain minimum size natural predation becomes less of a factor in its survival. Therefore the grassbed is diminished in importance as a refuge for

the larger crab, with the one important exception being the very vulnerable soft crab stages during the molting cycle. The reverse case would be that juveniles of a species are not protected by the vegetation but older individuals are. For example, the soft shell clam, *Mya arenaria*, lives near the sediment surface when their planktonic stages first set and the juveniles start to grow. With age, this species burrows deeper in the sediment. Because adult *Mya* are also found outside vegetated areas, we suggest that the minimum depth at which older *Mya* escape predation is less in vegetated areas than in non-vegetated areas because the rhizome mat would provide a physical barrier to the digging activities of predators such as the blue crab.

3. The refuge value of vegetation will be directly correlated with the density or biomass of the leaves (Heck and Orth, 1980a, b; Stoner, 1980a, b) for mobile species and for deeply burrowing ones it will be correlated with the density of the rhizome mat. The inceasing coverage offered by vegetation makes it more difficult for predators to effectively seek out and consume prey items, possibly interfering with potential behavioral patterns in these search strategies (Stoner, 1980b).

4. The refuge value of vegetation for a prey item will vary depending upon the foraging strategy of a particular predator. For example the refuge value for the prey of an ambush predator (i.e. one which sits and waits for prey items to pass by) may be different than that for a prey species fed upon by search predator (i.e. one which actively forages over a given area for prey items).

5. Different species of vegetation may have different refuge values depending on their morphology. We are suggesting that at the same density of plants per unit area of bottom, the more foliose species (i.e. those which are more highly branched or having a high ratio of surface area to biomass) have a greater reguge value than less foliose species. The degree of branching is directly related to amount of cover which allows prey species to effectively escape predation. Data from Heck's (1981) experiments showed grass shrimp, *Palaemonetes* spp., to have significantly higher survival rates in *Ruppia* vegetated areas than *Zostera* vegetated areas. According to Heck, *Ruppia* is more foliose than *Zostera* which would account for the increased survival of grass shrimp that he observed. In addition, field samples collected in a dense *Ruppia* bed by Heck yielded densities of grass shrimp higher than any samples collected from *Zostera* beds (Heck and Orth, 1980b; Heck, 1981).

Since the amount of branching and plant density are both critical factors in the survival of prey in grassbeds and different species of vegetation have different surface areas based on their morphology, we can hypothesize that a low density of a highly foliose species would have the same refuge value as a high density of a less foliose species. Stoner's data (1980c) is particularly relevant in that he concluded that blade surface area of macrophytes provides the best estimate of habitat complexity in seagrasses. This particular factor would be a critical one in management's option to replant vegetation. Because of the increased coverage afforded by more foliose species, the most viable option for replanting would be to use these species where possible.

In conclusion, beds of submerged aquatic vegetation play a distinct role in regulating the distribution and abundance of associated animals by their ability to mediate both predator-prey and competitive interactions. The degree of mediation will depend on the animal species in question and the density and morphology of the vegetation. This degree of interaction of the plant with its environment make submerged aquatic vegetation areas one of the most interesting and ecologically important systems in the marine environment.

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CHAPTER 4

SECONDARY PRODUCTION OF SOME DOMINANT MACROINVERTEBRATE SPECIES INHABITING A BED OF SUBMERGED VEGETATION IN THE LOWER CHESAPEAKE BAY

by

Robert Diaz

and

Tom Fredette

ABSTRACT

The production of the top 9 trophically important species to the higher level consumers at the Vaucluse Shores grassbed was 40.7 $g \cdot m^{-2} \cdot yr^{-1}$. This is a higher productivity than reported for most community production studies. If this rate of production is projected over the entire 140 hectare grassbed a total of 53 metric tons of dry tissue was produced and potentially available for consumption by other trophic levels. This also represents 6×10^{10} individuals which are born, grow, and die in a year. The average standing stock over the year was 4.6 metric tons leaving 48.4 metric tons to be accounted for.

The isopod *E. attenuata* accounted for 43% of the total production for the 9 species. The next two high ranking producers were *C. sapidus* and *G. mucronatus*, when combined with *E. attenuata* accounted for 84.8% of biomass produced by the 9 species. Turnover ratios were highest for *G. mucronatus* (24.5) and lowest for the snail *B. varium* (3.2).

INTRODUCTION

In addition to the spatial heterogeneity provided by the presence of submerged aquatic vegetation the most notable feature of these habitats is the high density of animals residing in the grass bed. This large standing crop of animals is thought to be fundamental to the resource value of submerged aquatic vegetation beds to migratory predators (crabs, fish, waterfowl) that utilize the beds for protection and as a feeding ground. However, one does not get an appreciation for the flow of energy needed to support the large populations of prey and predatory species by simply looking at the structural complexity of the populations at any given time. The amount of energy or biomass produced within the grass bed system can only be estimated by a detailed look at the secondary production of the individual species in the beds.

From our analysis of the feeding habits of the higher level consumers (fish and crabs) it is obvious that benthic invertebrates play a major role in the flux of energy through the seagrass system. The benthos then represent the major link between primary production, detritus, and higher trophic levels. Secondary production estimation is a very labor intensive process so we chose to focus on nine top tophically important benthic species to higher level consumers.

METHODS

Twelve consecutive monthly samples were taken for secondary production using a suction dredge (Fig. 1). Quantitative samples were collected from within a weighted plexiglass cylinder with a diameter of 28.6 cm (0.065 m^2) and a height of 65 cm. The cylinder was carefully placed over the grass blades and the sample was taken from within by filtering water through a plastic bag with a removable 0.5 mm mesh sieve bottom. Samples of larger, more motile, or widely spaced species were collected from within a weighted fiberglass cylinder 110 cm in diameter (0.95 m^2) and 30 cm high equipped with a 0.5 mm mesh screened top (Fig. 1). All samples from the larger fiberglass frame were filtered through a 1 mm x 1.5 mm mesh bag. The sampling frame was dropped from a boat over dense vegetation. Only drops over 100% vegetation cover were sampled. The majority of samples were taken from mixed *Zostera-Ruppia* areas. All samples were preserved in 10% buffered formalin. Samples were sorted in the laboratory and up to 200 complete individuals for each species per sample date were measured, dried and weighed. Based on their trophic importance to higher level consumers nine species were selected for production estimates:

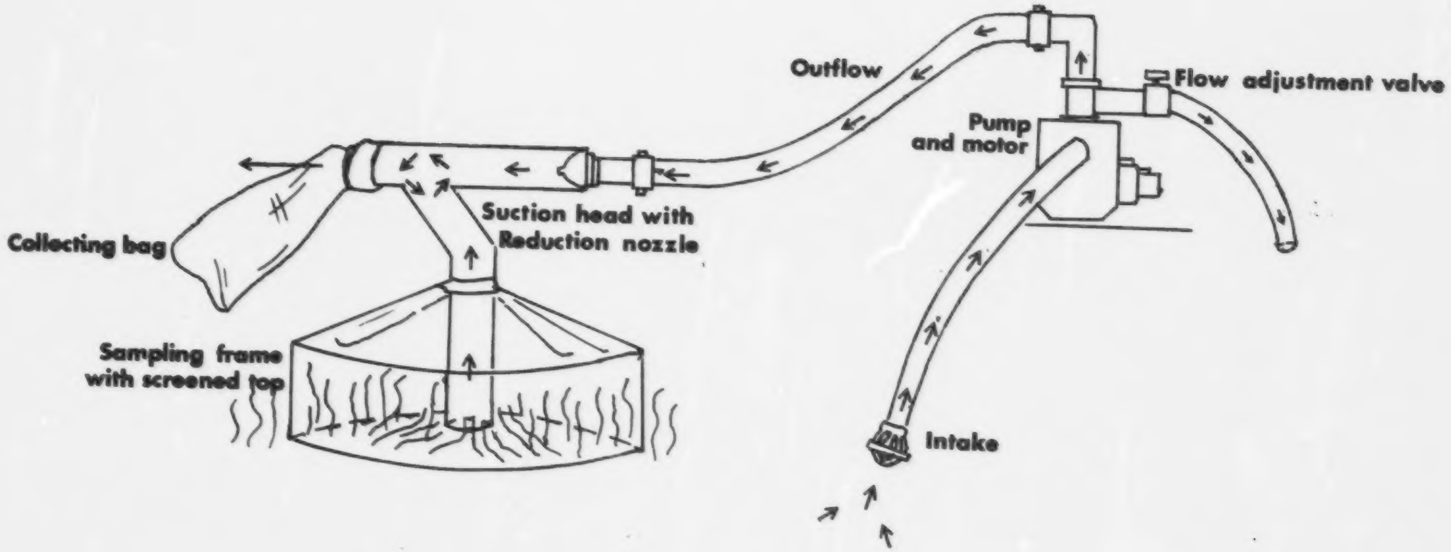
Outflow
Flow adjustment valve
Pump and motor
Suction head with Reduction nozzle
Collecting bag
Sampling frame with screened top
Intake

Fig. 1. Schematic diagram of suction dredge used for sampling secondary production species.

DECAPODS

Callinectes sapidus
Crangon septemspinosa
Palaemonetes vulgaris

MOLLUSCS

Bittium varium
Gemma gemma

ISOPODS

Erichsonella attenuata
Edotea triloba
Idotea balthica

AMPHIPODS

Gammarus mucronatus

Length-weight equations calculated for each species were based on dry weights (Table 1). Ash free dry weights (AFDW) were obtained by ashing known quantities of each organism in a muffle furnace at 500°F for 3 hours. Production for each species was determined with the size-frequency method (Hamilton 1969, Waters and Hokenstrom 1980, Hynes 1980) multiplied by the factor 365/CPI, where CPI is the cohort production interval or maturation period (Benke 1979). The instantaneous growth method (Waters 1977) was also used to calculate production of *Callinectes sapidus* and *Bittium varium*, for which cohorts were distinct.

Measurement data were partitioned into 6-12 size classes for each species and densities converted to individuals/m^2. With these data and length-weight equations (Table 1), mean size and weight were determined for each month and size class (Tables 2-10 and Fig. 2-4).

Species abundance data were analyzed graphically to determine population trends and sample variation. Population size-frequency distributions of replicate samples were tested with the non-parametric G-test (Sokal and Rholf 1969).

LIFE HISTORIES OF PRODUCTION SPECIES

Marine isopods are generally considered to be omniverous, scavenging a variety of plant and animal matter (Shultz 1969). Reproduction is by direct development of young within the marsupium of the female. The three isopods discussed here all occur within the grass bed as epifauna or epibenthos. *Edotea triloba*, common in eelgrass, is also associated with mud substrates. It is distributed from Virginia to Maine. *E. triloba* life spans seems to be about six months with peak recruitment from June to October. After spawning in the spring and early summer larger individuals disappear from the population (Fig. 2). *Erichsonella attenuata* has been reported from coral habitats as well as eelgrass. Its range extends from Connecticut to North Carolina (Shultz 1969). Ovigerous *E. attenuata* were present in the grassbed from May through January, peaking in July through September. Juvenile recruitment occurred from June to March. *Idotea balthica* has an amphi-Atlantic distribution occurring in the western Atlantic from the Gulf of St. Lawrence to South America. Strong and Daborn (1979) indicate that life span is slightly longer than one year in Canadian populations with juvenile recruitment in July. Ovigerous females were collected in the grassbed from May to November with juvenile recruitment occurring throughout this period and into December (Fig. 2).

TABLE 1. LENGTH-WEIGHT REGRESSIONS WHERE W IS THE PREDICTED DRY WEIGHT OF AN INDIVIDUAL WHOSE LENGTH MEASUREMENT IS L.

Species	Equation	n	r^2	Length measurement L
P. vulgaris	$w = 0.5880\ l^{2.53}$	43	0.92	carapace length
C. septemspinosa	$w = 0.5999\ l^{2.41}$	42	0.89	carapace length
C. sapidus	$w = 0.0643\ l^{2.74}$	71	0.96	carapace width
E. triloba	$w = 0.0070\ l^{2.87}$	52	0.84	head to telson
E. attenuata	$w = 0.0066\ l^{2.41}$	91	0.90	head to telson
I. balthica	$w = 0.0137\ l^{2.17}$	42	0.94	head to telson
G. mucronatus	$w = 0.1272\ l^{3.00}$	72	0.96	head plus 1st abdominal 3 segments
B. varium	$w = 0.0372\ l^{1.78}$	35	0.90	shell length
G. gemma	$w = 0.1039\ l^{1.56}$	13	0.91	shell height

TABLE 2. MONTHLY SIZE CLASS DATA FOR CALLINECTES SAPIDUS. INDIVIDUALS/10 m^2.

Size Classes (Lower Limits)	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	1979 Dec	1980 Jan	Feb	Mar	Total #/10 m^2	Mean Size (mm)	Mean Wt (mg)
0.0	18.2	18.6	1.2			3.5	73.8	54.4	28.2	46.5	42.5	14.6	301.5	6.8	15.2
10.0	21.1	20.7	5.8				10.4	37.6	24.1	45.2	33.2	43.9	242.0	12.2	64.6
20.0		3.1	4.7		1.3			2.6	1.3	2.7	2.7	1.3	19.7	23.1	366.1
30.0		1.0	9.3	3.9									14.2	34.9	1106.1
40.0				7.8	1.3	1.2	1.3						11.6	45.1	2210.4
50.0				3.9	1.3	2.3				1.3		1.3	10.1	55.9	3976.9
60.0			1.2	2.6			1.3					2.7	7.8	63.8	5705.2
70.0							1.3	1.3				2.7	5.3	74.5	8678.2
80.0				1.3								1.3	2.6	83.0	11658.3
Total #/10 m^2	39.3	43.5	22.2	19.6	3.9	6.9	88.1	95.9	53.6	95.7	78.4	67.8			
Mean Size (mm)	10.3	12.5	27.1	50.3	38.7	30.4	9.4	9.7	9.2	10.2	9.7	17.9			
Mean Wt (mg)	44.5	117.5	904.6	3422.9	1827.9	1871.9	271.4	146.3	38.8	86.3	44.7	931.5			

TABLE 3. MONTHLY SIZE CLASS DATA FOR CRANGON SEPTEMSPINOSA. INDIVIDUALS/10 m^2.

Size Classes (Lower Limits)		Months													Mean	Mean
										1979	1980			Total	Size	Wt
		Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	#/10 m^2	(mm)	(mg)
	1.0	0.6	4.1	4.7		1.3	4.6						1.5	15.3	1.6	2.1
	2.0	0.6	4.1	72.5	54.9	151.6	43.7	7.8					4.5	339.7	2.6	5.9
	3.0	0.6	1.0	36.2	23.5	99.7	76.0	36.3	5.2		1.5		3.0	283.0	3.3	11.1
	4.0	1.7	3.1	9.4	11.8	5.2	15.0	27.2	9.1				3.0	85.5	4.4	21.4
	5.0	7.4	3.1	2.3		2.6	2.3	19.4	15.5	3.0			3.0	58.6	5.4	35.1
	6.0	4.0	6.2	1.2				7.8	14.2	1.5			1.5	36.4	6.3	51.1
	7.0	2.3	5.2					2.6	11.7	7.6	1.5		1.5	32.4	7.4	75.3
	8.0	0.6	1.0								1.5			3.1	8.5	106.0
	9.0	0.6	2.1											2.7	9.6	138.6
	10.0												1.5	1.5	10.0	154.2
Total #/10 m^2		18.4	29.9	126.3	90.1	260.4	141.6	101.0	55.7	12.2	4.5	0	19.6			
Mean Size (mm)		5.7	5.3	3.0	3.0	2.9	3.2	4.4	5.8	6.8	6.6	0	4.4			
Mean Wt (mg)		43.8	44.4	9.1	9.1	8.3	10.7	23.0	44.0	62.3	67.5	0	32.2			

TABLE 4. MONTHLY SIZE CLASS DATA FOR PALAEMONETES VULGARIS. INDIVIDUALS/10 m^2.

		Months													
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	1979 Dec	1980 Jan	Feb	Mar	Total #10 m^2	Mean Size (mm)	Mean Wt (mg)
Size Classes (Lower Limits) 1.0				1.3	3.9	2.3				1.3			8.8	1.6	2.1
2.0				1.3	2.6	39.1	3.9	1.3		5.3	9.3		62.8	2.6	6.6
3.0	2.3	16.6		1.3	3.9	82.9	163.2	136.0	99.2	55.8	46.5	5.3	613.0	3.5	14.4
4.0	4.0	22.8	60.8	53.6	88.1	73.7	81.6	230.6	52.3	18.6	12.0	1.3	699.4	4.4	25.2
5.0	2.8	21.8	8.2	22.2	19.4	21.9	37.6	102.3	18.8	15.9	4.0		274.9	5.3	41.1
6.0	3.4	12.4	50.3	23.5	29.8	23.0	14.2	9.1	1.3	4.0			171.0	6.5	66.9
7.0		6.2	69.0	23.5			3.9	14.2					116.8	7.4	92.2
8.0		4.1	7.0	6.5									17.6	8.3	123.1
Total #/10 m^2	12.5	83.9	195.3	133.2	147.7	242.9	304.4	493.5	171.6	100.9	71.8	6.6			
Mean Size (mm)	4.6	5.3	6.3	5.7	4.8	4.0	4.2	4.5	4.0	3.9	3.6	3.7			
Mean Wt (mg)	29.9	44.3	65.7	52.8	33.5	23.1	24.2	27.7	20.5	21.0	16.0	17.3			

TABLE 5. MONTHLY SIZE CLASS DATA FOR *GEMMA GEMMA*. INDIVIDUALS/m^2.

Size Classes (Lower Limits)	Months														
									1979	1980			Total	Mean Size	Mean Wt
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	#/m^2	(mm)	(mg)
0.5	61.5	17.9	30.8	15.4	7.7	46.1	215.4	66.7	189.7	24.6	184.6	43.1	903.5	0.8	0.07
1.0	410.3	33.3	169.2	146.1	57.7	161.5	369.2	230.8	241.0	147.7	407.7	126.1	2500.6	1.2	0.15
1.5	271.8	100.0	200.0	215.4	100.0	184.6	353.8	194.9	220.5	138.5	492.3	126.1	2597.9	1.7	0.25
2.0	41.0	25.6	76.9	7.7	34.6	53.8	146.1	128.2	97.4	76.9	115.4	40.0	843.6	2.2	0.36
2.5	5.1	7.7	7.7		15.4	23.1	53.8	15.4	25.6	15.4	46.1	27.7	243.0	2.6	0.48
3.0							7.7		10.3	3.1		3.1	24.2	3.2	0.63
Total #/m^2	789.7	184.5	484.6	384.6	215.4	469.1	1146.0	635.3	784.5	406.2	1246.1	393.8			
Mean Size (mm)	1.5	1.7	1.7	1.6	1.8	1.6	1.5	1.6	1.4	1.6	1.5	1.6			
Mean Wt (mg)	0.19	0.25	0.24	0.22	0.26	0.22	0.20	0.22	0.19	0.23	0.20	0.22			

TABLE 6. MONTHLY SIZE CLASS DATA FOR BITTIUM VARIUM. INDIVIDUALS/m^2.

Size Classes (Lower Limits)	Months														
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	1979 Dec	1980 Jan	Feb	Mar	Total #/m^2	Mean Size (mm)	Mean Wt (mg)
1.0	4.4								3.8				8.2	1.4	0.07
1.5	54.9						56.4	23.1	84.6	30.8	12.3		262.1	1.8	0.11
2.0	76.9	9.2					148.7	61.5	103.8	101.5	36.9	36.9	575.4	2.2	0.15
2.5	8.8	52.3		5.1			20.5	11.5	19.2	9.2	6.1	6.1	138.8	2.7	0.22
3.0		178.5	10.3	5.1	15.4	5.1	25.6	11.5	30.8	12.3	6.1	9.2	309.9	3.3	0.30
3.5		150.8	46.2	20.5	18.5	10.3	5.1		11.5		6.1		269.0	3.7	0.38
4.0		33.8	92.3	76.9	24.6			3.8	7.7		6.1		245.2	4.2	0.48
4.5			61.5	97.4	12.3								171.2	4.7	0.59
5.0			87.2	82.1	6.1								175.4	5.2	0.70
5.5			5.1	46.2	3.1								54.4	5.6	0.80
6.0				10.3									10.3	6.2	0.95
6.5				5.1									5.1	6.5	1.03
Total #/m^2	145.0	424.6	302.6	348.7	80.0	15.4	256.3	111.4	261.4	153.8	73.6	52.2			
Mean Size (mm)	2.1	3.4	4.6	4.8	4.2	3.7	2.3	2.3	2.3	2.2	2.6	2.4			
Mean Wt (mg)	0.14	0.34	0.56	0.62	0.48	0.37	0.16	0.17	0.18	0.15	0.21	0.18			

TABLE 7. MONTHLY SIZE CLASS DATA FOR IDOTEA BALTHICA. INDIVIDUALS/m^2.

Size Classes (Lower Limits)	Months												Total	Mean Size	Mean Wt
									1979	1980					
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	#/m^2	(mm)	(mg)
1.0		1.5	23.0	61.4	1.9	7.7	11.5	17.6	26.9	9.2		12.3	172.8	2.0	0.06
3.0			53.7	138.3	13.5	19.2	26.9	28.6	69.2	64.6	3.1	40.0	457.1	3.6	0.24
5.0			51.1	105.0	46.1	13.5	19.2	22.0	23.0	27.6	6.1	33.8	385.5	5.6	0.59
7.0			51.1	48.6	34.5	5.7	19.2	26.4	3.8	12.3	3.1	30.8	235.5	7.6	1.17
9.0		1.5	10.2	28.2	13.5	1.9	7.7	24.2	11.5	30.8	3.1	9.2	141.8	9.6	1.95
11.0		1.5	2.6		5.7			11.0	19.2	6.2	3.1	6.1	55.4	11.7	3.03
13.0							3.8	2.2		24.6			30.6	13.6	4.22
15.0		4.6					3.8	2.2	7.7	6.2		3.1	27.6	15.7	5.79
17.0		1.5										3.1	4.6	17.8	7.64
Total #/m^2	0	10.6	191.8	381.5	115.2	48.0	92.1	134.2	161.3	181.5	18.5	175.3			
Mean Size (mm)	0	12.6	5.3	4.5	6.5	5.5	6.4	6.9	5.9	7.3	8.0	6.0			
Mean Wt (mg)	0	4.26	0.66	0.48	0.94	0.67	1.12	1.22	1.03	1.49	1.50	0.95			

TABLE 8. MONTHLY SIZE CLASS DATA FOR *GAMMARUS MUCRONATUS*. INDIVIDUALS/m^2.

	Months														
									1979	1980				Mean	Mean
Size Classes (Lower Limits)	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Total #/m^2	Size (mm)	Wt (mg)
0.5	85.7	442.3	125.3	54.9	26.9	42.3	25.0	65.4	192.3	138.5	353.8	246.1	1798.5	0.7	0.06
1.0	30.8	253.8	184.6	44.0	48.1	23.1	13.5	55.8	184.6	134.6	123.1	189.7	1285.8	1.2	0.22
1.5	30.8	257.7	79.1	22.0	19.2	13.5	7.7	26.9	84.6	134.6	117.9	179.5	973.5	1.7	0.63
2.0	57.1	96.2	15.4	2.2	1.9	1.9	3.8	23.1	65.4	157.7	66.7	117.9	609.2	2.2	1.36
2.5	28.6	73.1							38.5	92.3	66.7	41.0	340.1	2.7	2.43
3.0	6.6	69.2							7.7	42.3	20.5	46.1	192.5	3.2	4.03
3.5	4.4	26.9								11.5	10.3	10.3	63.4	3.6	6.13
4.0		3.8									5.1		9.0	4.1	8.78
4.5		3.8											3.8	4.6	12.38
Total #/m^2	213.2	1226.9	404.4	123.1	96.2	80.8	50.0	171.2	573.1	711.5	764.1	830.6			
Mean Size (mm)	1.6	1.5	1.2	1.1	1.2	1.1	1.1	1.2	1.4	1.8	1.4	1.5			
Mean Wt (mg)	0.96	0.88	0.28	0.23	0.27	0.21	0.27	0.34	0.56	1.13	0.74	0.83			

TABLE 9. MONTHLY SIZE CLASS DATA FOR ERICHSONELLA ATTENUATA. INDIVIDUALS/m^2.

Size Classes (Lower Limits)	Months												Total #/m^2	Mean Size (mm)	Mean Wt (mg)
									1979	1980					
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar			
1.5			261.5	396.2	353.8	215.4	261.5	123.1	30.8	5.1	7.7	3.1	1631.2	2.4	0.05
3.0	7.7		192.3	130.8	300.0	220.5	384.6	117.9	102.6	30.8	53.8	21.5	1562.5	3.7	0.15
4.5	17.9		165.4	84.6	284.6	456.4	469.2	76.9	117.9	97.4	246.2	80.0	2096.5	5.2	0.35
6.0	33.3	46.2	123.6	153.8	238.5	220.5	469.2	215.4	261.5	200.0	346.2	141.5	2449.2	6.7	0.66
7.5	28.2	147.7	11.5	265.4	561.5	271.8	300.0	261.5	369.2	292.3	400.0	147.7	3056.8	8.2	1.06
9.0	23.1	233.8		96.2	169.2	159.0	100.0	76.9	174.4	235.9	238.5	132.3	1639.3	9.6	1.55
10.5	10.3	236.9	23.1	76.9	46.2	30.8	15.4	61.5	71.8	112.8	46.2	27.7	759.6	11.1	2.21
12.0	7.7	64.6	23.1	30.8	30.8	25.6	7.7	5.1		30.8		6.2	232.4	12.5	2.90
13.5		36.9		7.7	7.7		7.7		5.1	10.3			75.4	13.9	3.79
15.0		18.5							5.1				23.6	15.5	4.88
16.5		6.2	3.8	3.8									13.8	16.8	5.97
Total #/m^2	128.2	790.8	803.4	1246.2	1992.3	1600.0	2015.3	938.3	1138.4	1015.4	1338.6	560.0			
Mean Size (mm)	7.9	10.3	4.6	5.9	6.1	6.0	5.6	6.7	7.5	8.3	7.4	7.7			
Mean Wt (mg)	1.11	1.95	0.41	0.74	0.69	0.64	0.53	0.80	0.97	1.20	0.91	1.01			

TABLE 10. MONTHLY SIZE CLASS DATA FOR EDOTEA TRILOBA. INDIVIDUALS/m^2.

	Months														
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	1979 Dec	1980 Jan	Feb	Mar	Total #/m^2	Mean Size (mm)	Mean Wt (mg)
Size Classes (Lower Limits) 1.0		30.8	110.8	203.8	346.1	292.3	669.2	223.1	138.5		10.3	7.7	2032.6	1.7	0.03
2.0	2.2		227.7	326.9	869.2	211.5	1007.7	1115.4	792.3	169.2	56.4	253.8	5032.3	2.5	0.10
3.0	19.6	15.4	178.5	146.2	415.4	161.5	100.0	353.8	400.0	430.8	425.6	661.5	3308.3	3.4	0.24
4.0	34.8	76.9	15.4	15.4	53.8	46.2	15.4	61.5	46.1	164.1	256.4	100.0	886.0	4.4	0.49
5.0	6.5	44.6		15.4			7.7			15.4	87.2	46.1	222.9	5.3	0.85
6.0	2.2	6.2		3.8						25.6	30.8	23.1	91.7	6.3	1.40
7.0	2.2	6.2								5.1	10.3		23.8	7.2	2.02
Total #/m^2	67.5	180.1	532.4	711.5	1684.5	711.5	1800.0	1753.8	1376.9	810.2	877.0	1092.2			
Mean Size (mm)	4.5	4.1	2.7	2.3	2.6	2.3	2.2	2.6	2.7	3.6	4.0	3.4			
Mean Wt (mg)	0.61	0.53	0.14	0.09	0.13	0.11	0.08	0.13	0.15	0.33	0.43	0.28			

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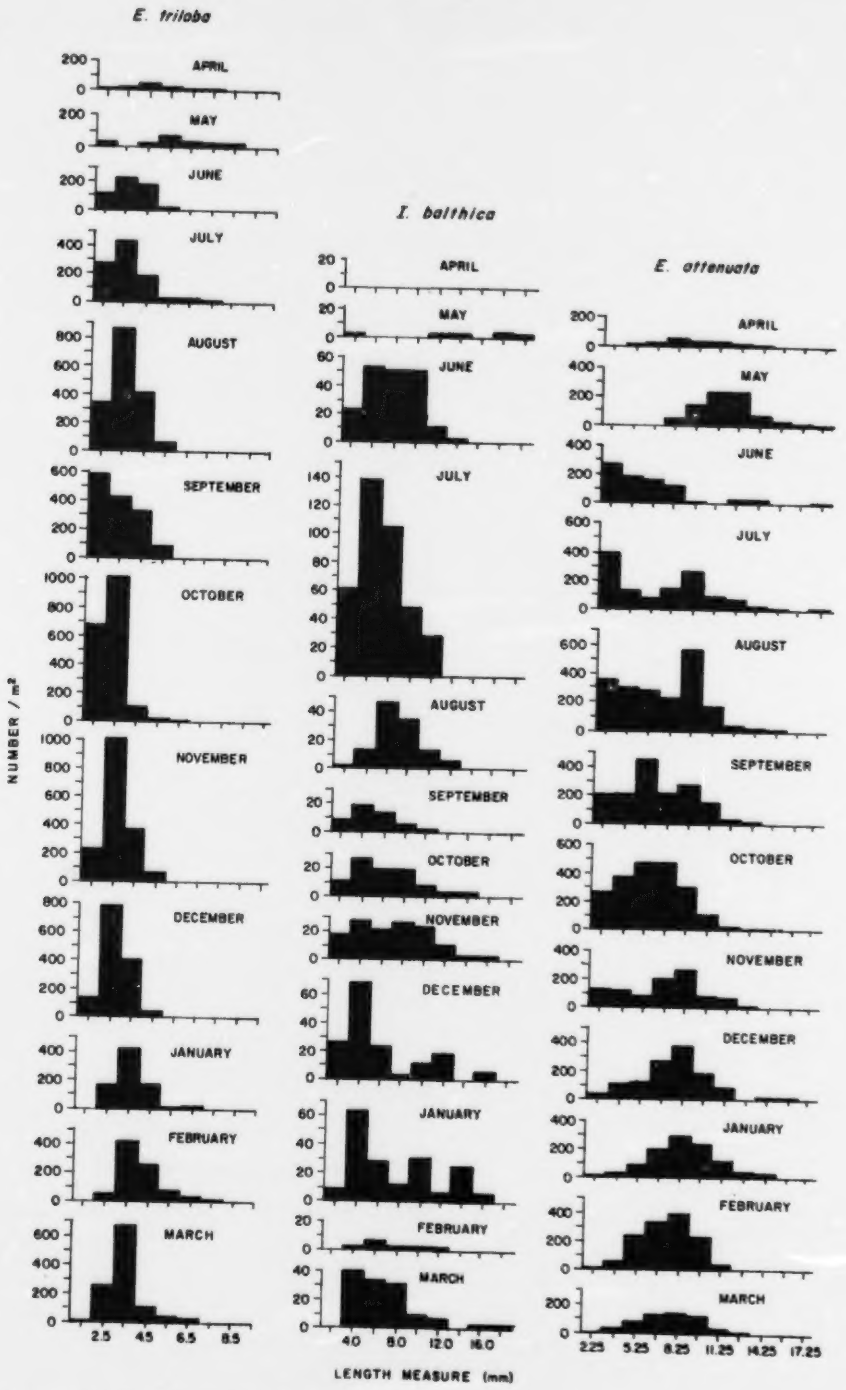

Fig. 2. Monthly size-frequency data for _Edotea triloba_, _Idotea balthica_ and _Erichsonella attenuata_.

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Gammarus mucronatus is a shallow water amphipod distributed from the Gulf of St. Lawrence to the Gulf of Mexico (Bousfield 1972). It is eurytopic and can be found associated with algae, fouling communities, *Spartina* marshes (Van Maren 1978, Borowsky 1980), and eelgrass (Marsh 1973). It has a generalized diet consisting of both macro- and microphytes (Zimmerman et al. 1979). Development of juveniles is direct and occurs within the marsupium of the female. Ovigerous females were collected and juvenile recruitment occurred throughout the year. From June to October greater than 10% of the total population was ovigerous (range 11-23%) with less than 10% of the population ovigerous in all other months (range 3-8%). Based on laboratory study life span is estimated to be approximately four months.

The filter feeding bivalve, *Gemma gemma* is generally found in well sorted fine sand. It is distributed from Nova Scotia to Texas (Abbott 1974). Maximum lifespan is approximately two years. Reproduction is ovoviviparous (young are brooded). Sellmer (1967) determined the mean size of juvenile length at release to be 410 u. New England and mid-Atlantic populations release juveniles from June to August (Sellmer 1967, Green and Hobson 1970). However, the growth rates for the two areas are quite different. One year old individuals from New England were estimated to be 1.6 mm (Green and Hobson 1970) and 4.1 mm long along the mid-Atlantic coast (Sellmer 1967). Continuous reproduction and rapid growth of *G. gemma* at the Vaucluse Shores site clouded cohort separation (Fig. 3). The actual growth rate or life span of *G. gemma* would not be determined. The model size throughout the year was 1.25 to 1.75 mm with no individual ever being larger than 3.25 mm.

The prosobranch gastropod *Bittium varium* inhabits eelgrass beds from Chesapeake Bay south to Florida, Texas, and the West Indies (Wulff 1970). It is thought to be primarily a detritivore or algivore. Marsh (1976) observed egg masses present on grass blades in May and June with recruitment beginning in late June and lasting into the fall. Lifespan is approximately one year, the newly recruited population overwintering close to the bases of *Zostera marina* turions or within the sediment (Wulff 1970, Marsh 1976). Recruitment was observed in the fall, from October to December (Fig. 3).

The grass shrimp *Palaemonetes vulgaris* is distributed in shallow coastal and estuarine waters from Massachusetts to Texas (Williams 1965). Population migration from *Zostera marina* beds to sandy-shell bottoms has been reported (Thorp 1976). *Palaemonetes vulgaris* is an opportunistic omnivore often consuming large quantities of detritus, digesting the associated bacteria, fungi and protozoans (Adams and Angelovic 1970).

Knowlton and Williams (1970) reported ovigerous females occurring from February to October in North Carolina populations with recruitment of juveniles beginning in June. These new recruits grow quickly and may spawn in the late summer. The Vaucluse Shore populations have a slightly less extensive breeding season from June to September with recruitment occurring from July to September (Fig. 4).

The decapod *Crangon septemspinosa* has a shallow water (0-35 m) subarctic-boreal distribution. It occurs on the North American Atlantic Coast from Baffin Bay to eastern Florida (Williams 1965). *C. septemspinosa* is

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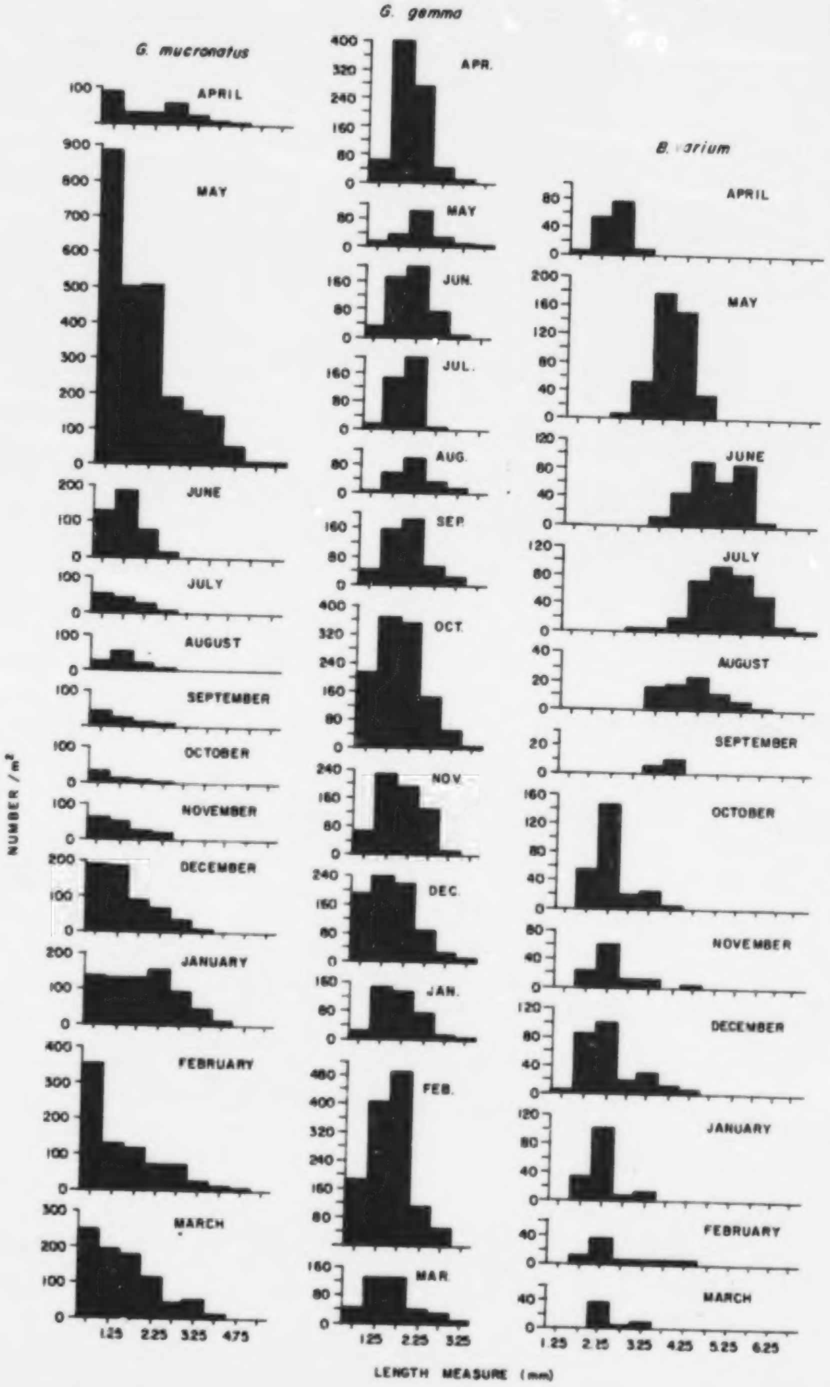

Fig. 3. Monthly size-frequency data for Gammarus mucronatus, Gemma gemma and Bittium varium.

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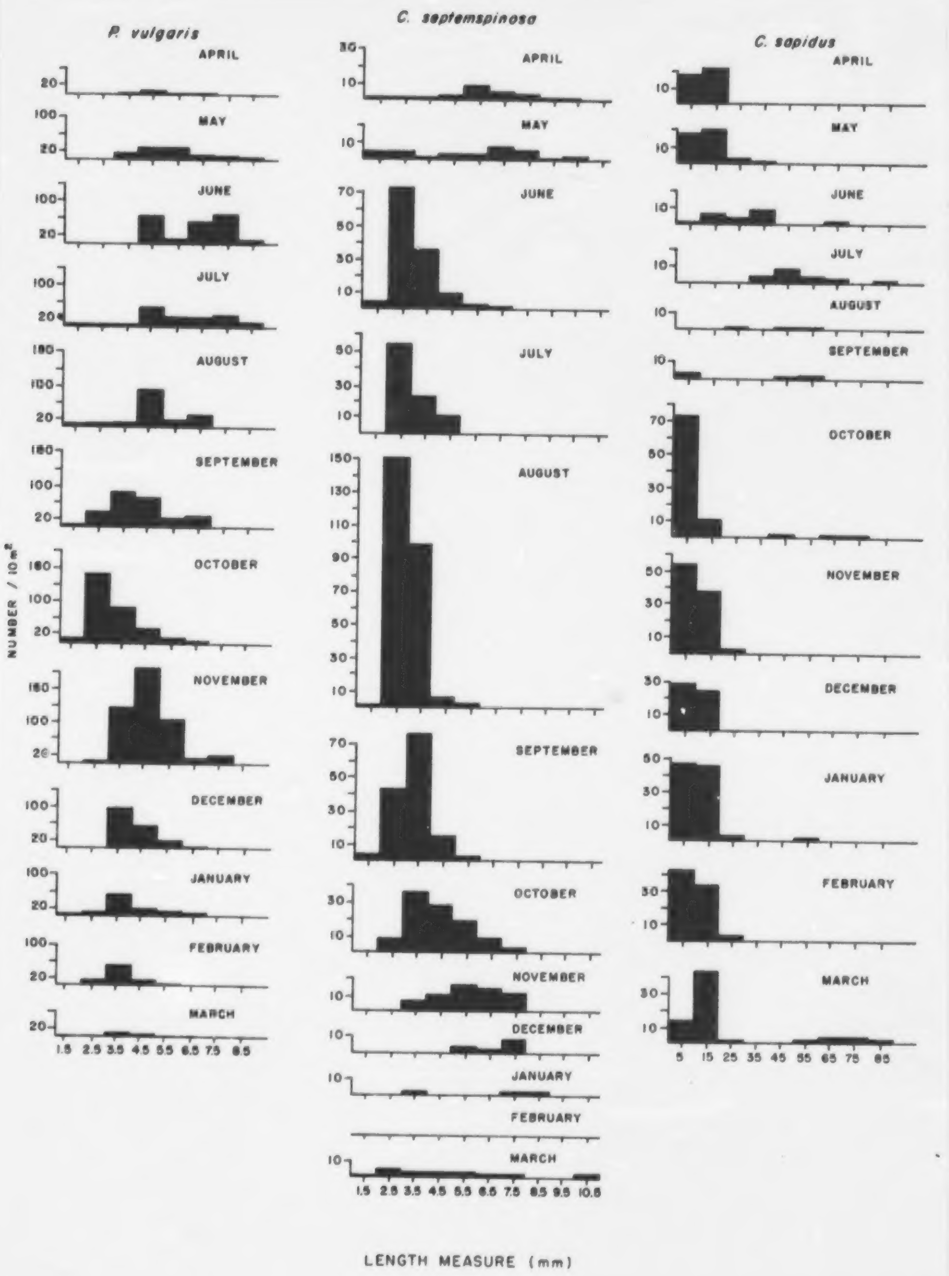

Fig. 4. Monthly size-frequency data for Palaemonetes vulgaris, Crangon septemspinosa and Callinectes sapidus.

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eurytopic inhabiting a general salinity range of 10-31‰. It undergoes migrations to deeper water in response to low temperatures (Haefner 1979). *C. septemspinosa* is a nocturnal feeder with an opportunistic feeding strategy. It can be a detritivore scavenger or predator. Predation on mysids accounts for large portions of the diet for some populations (Welsh 1970).

Regionally, *C. septemspinosa* seems to have a single extended breeding period from October to June with a March-April peak (Haefner 1979). Eggs are brooded by the females for a short period after which development of planktonic larvae occurs. Larvae are present in the plankton throughout the year with a mid winter to early spring maximum. Lifespan has been estimated at 2.5 years from studies of more northerly populations (Haefner 1979). In the grassbed ovigerous females were observed only from March to June followed by recruitment in June through August. Much of the winter population decline may be due to migration to deeper channel areas (Fig. 4).

Callinectes sapidus is distributed in shallow coastal and estuarine waters (0-35 m) from Nova Scotia south to northern Argentina (Williams 1974). The species is euryhaline occurring in fresh water to hyperhaline lagoons. Trophically, *C. sapidus* can best be described as an opportunistic omnivore. Life span is up to 3.5 years. Recruitment of juveniles begins in August and continues into the fall months. Mating occurs from May to October with spawning delayed two to nine months and occurring from May to September of the following year (Van Engel 1958). Spawning activity is concentrated near the mouths of estuarine and shallow coastal waters (Williams 1974). Recruitment at the grassbed occurred in September and continued through November (Fig. 4).

RESULTS AND DISCUSSION

Abundance data were analyzed by determining median and semi-interquartile range for replicate samples (Fig. 5). The distribution of most species was typically patchy. Most of the species exhibited one major annual population maximum. *P. vulgaris*, *C. septemspinosa*, *G. mucronatus* and *I. balthica* showed the least month to month variability. The other 5 species fluctuated widely from month to month. This type of variation is indicative of spatial heterogeneity that may be related to patchiness of populations or migration.

Analysis of size-frequency distributions of replicate samples was done for *E. triloba* and *G. mucronatus*. These two species were chosen because it was thought that microhabitat parameters could have greater influence on the population structure of species with relatively short maturation times and extended breeding periods. Significant differences existed in four of eight months for *E. triloba* and in two of seven months for *G. mucronatus* (Table 11). To further identify where variation in size frequency distributions was occurring samples from pure stands of *Zostera* and *Ruppia* were eliminated leaving only samples from the mixed grassbed habitat. Results indicated that much of the variation in size frequency distribution was related to vegetation type. All months that were different when all habitats were combined were now not different. However, there were still two months for each species where the replicates from the mixed grassbed were different. These differences were due mainly to variation in the number of smaller size class individuals between replicates.

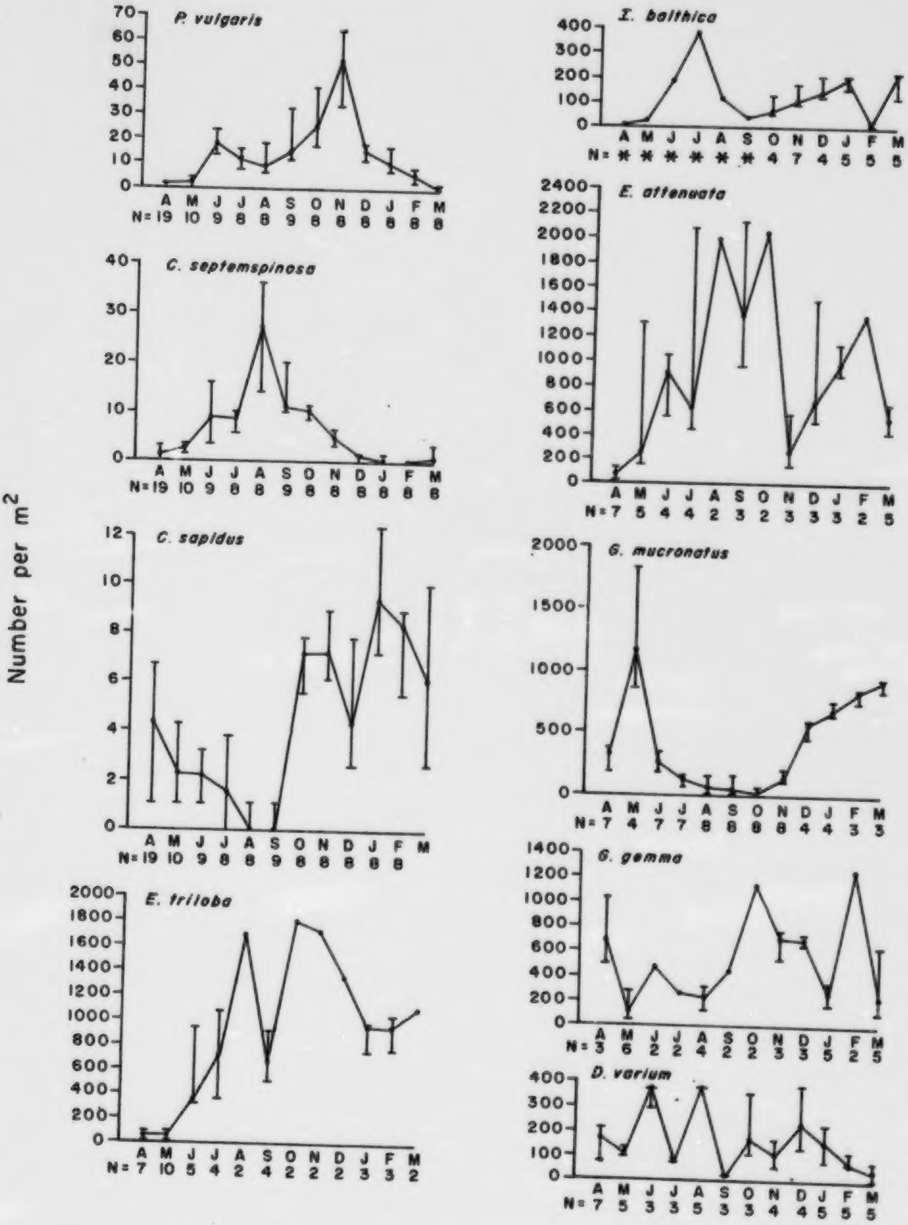

Fig. 5. Monthly abundance data: median (.) and 1st and 3rd quartiles (I) indicated. N = number of samples; * = data for individual sample lost.

TABLE 11. RESULTS OF G-TEST COMPARISONS. *$p \leq 0.05$, *$p \leq .01$

All Replicates includes *Zostera*, *Ruppia*, and mixed grassbed samples

	G. mucronatus	*E. triloba*		*G. mucronatus*	*E. triloba*
Apr	*	n.s.	Oct	n.s.	--
May	**	n.s.	Nov	n.s.	--
Jun	*	n.s.	Dec	--	--
Jul	*	*	Jan	--	--
Aug	n.s.	--	Feb	--	--
Sep	n.s.	**	Mar	--	--

Only mixed grassbed samples

	G. mucronatus	*E. triloba*		*G. mucronatus*	*E. triloba*
Apr	n.s.	n.s.	Oct	n.s.	n.s.
May	n.s.	n.s.	Nov	n.s.	**
Jun	n.s.	n.s.	Dec	n.s.	n.s.
Jul	n.s.	n.s.	Jan	*	n.s.
Aug	n.s.	**	Feb	**	n.s.
Sep	n.s.	n.s.	Mar	n.s.	n.s.

N.S. - Not significant

* - $p \leq 0.05$

** - $p \leq 0.01$

- Only samples from mixed grassbed habitat were collected.

Production estimates using the size-frequency method for the nine species are based on combined data from all three habitats (Table 12). Secondary production by *E. attenuata* was found to be greatest, amounting to 43% of the total production for the nine species. The next two high ranking producers, *C. sapidus* and *G. mucronatus*, when combined with *E. attenuata* accounted for 84.8% of the biomass produced by these nine species. The contributions by *E. attenuata* and *G. mucronatus* can be attributed to their relatively high turnover rates (P/B), 18.9 and 24.5 respectively. While *C. sapidus* P/B ratio was low its standing stock was high (Table 12).

Since *C. sapidus* could be traced as a single cohort production was also estimated by the instantaneous growth method, which yields 15.8 $g\cdot.m^{-2}\cdot yr^{-1}$. *C. sapidus* would then account for 33% of the production, as opposed to 22% based on the size-frequency method, and the top three species would account for 87%. The difference between these two estimates illustrates the difference that can occur by the application of different methods. The results for *B. varium* show that the instantaneous growth method (0.2 $g\cdot m^{-2}\cdot yr^{-1}$) does not necessarily produce larger estimates than the size-frequency method, as in this case there is close agreement. In the case of *C. sapidus* only production for a small portion of its life span was calculated, which lead to the discrepancy in values.

Four species that were moderately abundant in the community but were not used for secondary production estimates are the amphipods *Ampithoe longimana*, *Cymadusa compta*, *Microprotopus raneyi* and the gastropod *Astyris lunata*., For these species and the nine production species wet weight biomass was determined from the routine baseline epifaunal and infaunal samples. Wet weight biomass was converted to dry weight biomass using a conversion factor of 0.17 (Waters 1977) (Table 13). It can be noted that for the secondary production species there is at times disagreement between the mean dry weights obtained from the secondary production data and that from the routine data. This can probably be attributed to the patchiness of distributions and the different amounts of information contained in each mean. The routine baseline biomass data were next converted to production values by multiplying the P/B ratios determined from this study. For the amphipods the P/B ratio of *G. mucronatus* was used and for *A. lunata* the ratio from *B. varium* (Table 10).

The total production based on routine sampling was 18 $g\cdot m^{-2}\cdot yr^{-1}$ estimated from the monthly samples excluding the decapods. The difference is due to the quarterly sampling not being able to discern turnover shorter than 3 months. All the amphipods and isopods turnover at much shorter intervals, on the order of weeks in the summer. Quarterly sampling does not accurately estimate biomass and tends to yield conservative production values (compare tables 12 and 13). For *B. varium* which has a lower turnover rate quarterly samples do accurately estimate production. For *G. gemma* mean biomass was twice as high in the quarterly samples yielding twice the production of monthly samples. *G. gemma* was simply much more abundant in the quarterly samples. Its higher turnover rate (Table 12) and irruptive populations would tend to indicate that both the quarterly and monthly samples underestimated its population.

TABLE 12. PRODUCTION ESTIMATES BASED ON THE SIZE FREQUENCY METHOD (HYNES 1980). P = PRODUCTION IN GRAMS DRY WT; AFDW P = PRODUCTION IN ASH FREE DRY WEIGHT; P/B = TURNOVER RATIO; $\overline{B}$ = MEAN BIOMASS; CPI = COHORT PRODUCTION INTERVAL.

Species	P g.m^{-2}yr-1	% Total P	AFDW P g.m^{-2}yr-1	$\overline{B}$ g.m^{-2}	N P/B	CPI days
P. vulgaris	1.8	4.4	1.54	0.520	3.4	365
C. septemspinosa	0.5	1.2	0.43	0.119	4.4	365
C. sapidus	8.9	21.9	5.11	1.908	4.7	365
E. triloba	2.0	4.9	1.31	0.175	11.3	182
E. attenuata	17.6	43.2	14.86	0.938	18.9	91
I. balthica	1.0	2.4	0.80	0.116	8.5	203
G. mucronatus	8.0	19.7	6.89	0.327	24.5	91
B. varium	0.2	0.5	—	0.062	3.2	365
G. gemma	0.7	1.7	—	0.125	5.9	182
	40.7 g.m^{-2}yr^{-1}					

TABLE 13. DRY WEIGHT BIOMASS DETERMINATIONS (G.M^{-2}) FROM THE BASELINE PORTION OF THE SAV STUDY. THE PRODUCTION WAS DETERMINED FROM P/B RATIOS.

Species	4/79	6/79	9/79	11/79	Mean	Production
E. triloba	0.18	0.14	0.11	0.13	0.13	1.5
I. balthica	0.02	0.05	0.08	0.12	0.07	0.6
E. attenuata	0.23	0.28	0.48	0.74	0.42	7.9
G. mucronatus	0.37	0.15	0.05	0.05	0.15	3.7
A. longimana	0.01	0.00	0.01	0.02	0.01	0.2
C. compta	0.01	0.03	0.12	0.13	0.05	1.2
M. raneyi	0.04	0.04	0.02	0.03	0.03	0.7
B. varium	0.09	0.15	0.02	0.03	0.07	0.2
A. lunata	0.05	0.13	0.01	0.06	0.09	0.5
G. gemma	0.15	0.51	0.26	0.16	0.26	1.5
					Total	18.0

The nine species examined produced a total of 40.7 g dry wt$\cdot m^{-2} yr.^{-1}$ which is a high production value. While there are no other grass bed studies for comparison these nine species were found to be more productive then most community production studies from both freshwater and marine systems (Waters 1979). To put this high rate of production into perspective we project the 40.7 $g\cdot^{-2}\cdot yr^{-1}$ to the entire 140 hectare grass bed., making the basic assumption that production of the nine species would be uniform over the entire bed. A total of 53 metric tons of dry tissue was then produced and potentially available for consumption by other trophic levels, which could be either higher level consumers or lower level decomposers. This represents approximately 60,000,000,000 individuals which are born, grow, and die in the grass bed each year (Table 14). Our estimates are most likely conservative since they represent only 9 of well over 75 trophically or numerically dominant species in the grass bed system. Also our monthly sampling program tended to underestimate production of those species (amphipods and isopods in particular) which turned over in less than a month. Gammarus mucronatus, as an example, in the lab grew to reproductive size in less than two weeks from marsupial release at 17°C. In the field under more optimal growing conditions growth may be even faster and turnover higher.

The importance of this high secondary productivity to fish and crab predators is intuitive, but the portion of the production which goes to predators is unknown. On average there are 4.6 metric tons of standing stock over the year in the grass bed. This leaves 48.4 metric tons to be accounted for.

Table 14. PRODUCTION ESTIMATES PROJECTED FOR THE ENTIRE VAUCLUSE SHORES GRASS BED (AREA = 140 HECTARES).

	Biomass Produced/Year	# of Individuals Produced/Year
G. mucronatus	11.2×10^3 Kg	2.0×10^{10}
G. triloba	2.8×10^3	1.1×10^{10}
E. attenuata	24.6×10^3	2.7×10^{10}
I. balthica	1.4×10^3	1.1×10^9
P. vulgaris	2.5×10^3	8.1×10^7
C. septemspinosa	0.74×10^3	2.3×10^8
C. sapidus	12.5×10^3	1.5×10^7
B. varium	0.28×10^3	9.5×10^8
G. gemma	0.98×10^3	4.5×10^9
Total	53.0×10^3 Kg	6.1×10^{10}

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CHAPTER 5

PRELIMINARY STUDIES OF GRAZING BY *BITTIUM VARIUM* ON EELGRASS PERIPHYTON[1]

by

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ABSTRACT

The grazing activities of *Bittium varium* Pfeiffer on periphyton colonizing live eelgrass (*Zostera marina* L.) and artificial eelgrass (polypropylene ribbon) were investigated. Quantitative measurements of grazing impact on artificial substrates were determined by periphyton pigment extraction and dry weight differences between grazed and ungrazed blades. Significant differences occurred in phaeophytin and dry weight calculations but chlorophyll *a* measurements were not significantly different. This suggests that senescent diatoms constituted the bulk of the periphyton weight and were selectively removed over more actively photosynthesizing diatoms.

An examination of scanning electron micrographs further elucidated the impact of grazing by *Bittium varium*. Some micrographs revealed that *B. varium* removed primarily the upper layer of the periphyton crust on both artificial substrates and living *Zostera marina*. The diatom *Cocconeis scutellum* Ehrenb. which attaches firmly to living *Z. marina* blades was less commonly removed than *Nitzschia* or *Amphora*. Through its grazing activities, *B. varium* may maintain community dominance by tightly adhering diatoms such as *C. scutellum*. Evidence of the complete removal of periphyton exposing the *Z. marina* epithelium, was revealed in other micrographs.

The grazing activities of *Bittium varium* which removes periphyton from seagrass blades, could have important implications for the distribution and abundance of *Zostera marina* in the Chesapeake Bay.

INTRODUCTION

The term grazing is generally used in terrestrial and aquatic ecological studies to indicate herbivory. Grazing food webs in terrestrial ecosystems are more easily studied and have historically received greater attention than those in the aquatic realm (Crisp, 1964). However, in recent years, an emphasis has been placed on understanding such relationships in both freshwater and marine habitats.

Primary producers in aquatic systems include planktonic and benthic microalgae (e.g. diatoms), macroscopic algae, and both submerged as well as emergent macrophytes. The majority of energy fixed by the latter two groups is generally not directly utilized by invertebrate herbivores and enters the food chain via a detrital pathway (Teal, 1962; Harrison and Mann, 1975; Tenore, 1975; Tenore et al., 1977). Phytoplankton and benthic microalgae constitute the major sources of energy fixed by primary producers that is available for direct transfer to higher trophic levels (Steele, 1974).

Many of the original investigations on aquatic grazing dealt with microplanktonic crustaceans and their influence on phytoplankton populations (Marshall and Orr, 1955; Porter, 1977). Similar studies on the effects of benthic grazers have received more recent attention.

Grazing studies of benthic aquatic herbivores emphasize their impact on both macro- and microscopic plant communities. Herbivorous fishes (Stephenson and Searles, 1960; Randall, 1965; Earle, 1972; John and Pope, 1973), sea urchins (Margalef and Rivero, 1958; Leighton et al., 1965; Jones and Kain, 1967; Paine and Vadas, 1969; Breen and Mann, 1976) and gastropod mollusks (Randall, 1964; Southward, 1964; Kain and Svedsen, 1969; Dayton, 1971; Lein, 1980) have a dramatic effect on biomass and species composition of macroalgae or marine vascular plants.

Herbivore-plant interactions involving microalgal communities are somewhat less well studied (Nicotri, 1977). The nutritional importance of benthic marine diatoms in the diet of the marsh snail, *Ilyanassa obsoleta*, has only recently been established (Wetzel, 1977). Castenholz (1961) demonstrated the drastic reduction in biomass of intertidal epilithic diatoms in the presence of the grazing mollusks, *Littorina scultata* and *Acmaea* spp. A similar result was demonstrated and selective removal of both the outermost portion of the diatom mat and the more loosely adhering species was shown to occur when four intertidal gastropod species grazed on diatom colonized artificial substrates (Nicotri, 1977). In contrast, studies by Kitting (1980) showed that even under high experimental grazer (*Acmaea scutum*, a gastropod) densities, the principal algal species preyed upon did not detectably decrease. Algal declines were instead attributed to physical factors.

Kitting (1980) also found that *A. scutum* fed on a mixed diet of two encrusting algal species in a fixed proportion even over a wide range of availabilities of the two foods. None of these studies, however, dealt with the effects of grazing activities on diatom colonized living substrates such as submerged aquatic vegetation.

Grazing by marine herbivores may have important implications when the colonized substrates are submerged aquatic plants. A covering of epiphytes can significantly reduce the photosynthetic rate of the macrophyte by acting both as a barrier to carbon uptake and by reducing light intensity. Eelgrass (*Zostera marina*) experienced a 45% reduction in photosynthesis under optimal light intensity because of diatoms, mostly *Cocconeis scutellum*, that formed a thick crust covering the plant (Sand-Jensen, 1977). A dense growth of epiphytes and associated micro-organisms (i.e. periphyton sensu Weitzel, 1979) which proliferates under nutrient enriched conditions has been implicated as the cuase for macrophyte declines in both freshwater (Phillips et al., 1978; Moss, 1981; Eminson and Moss, 1981) and marine (Sand-Jensen, 1977) environments. The extent of periphytic fouling may also determine the lower depth limit of occurrence for macrophytes by shading during the months with reduced solar illumination (Larkum, 1976).

Grazing organisms could be important in controlling periphyton proliferation (Mook, 1977) and by their feeding activities may indirectly enhance the distribution and abundance of the marophytes. This complex relationship has not been thoroughly ivestigated although Greze (1968) and Zimmerman et al. (1977, 1979) demonstrated that some gammaridean amphipods in seagrass communities feed almost exclusively on seagrass epiphytes. Morgan (1980) showed that epiphytes of the seagrass, *Halodule wrightii*, and not the grass itself were important in the diet of the grass shrimp, *Palaemonetes pugio*. More detailed laboratory studies of grazing effects on *Zostera marina* periphyton indicated that the amphipod, *Caprella laeviuscula*, caused a very significant reduction in periphyton biomass when compared to ungrazed blades (Caine, 1980). It was further stated in this study that *C. laeviuscula*, by its grazing activities, "allowed *Z. marina* to grow in areas where it would otherwise have been excluded by periphyton."

Studies on interactions between *Zostera marina* associated periphyton, and grazers in Chesapeake Bay seagrass ecosystems have particular relevance in light of the recent local declines of this important marine grass (Orth et al., 1979). One of the dominant members of the *Z. marina* epifaunal community is the small gastropod, *Bittium varium* Pfeiffer (Cerithiidae) (Marsh, 1973, 1976). This species has a life cycle of 1.5 years, grows to a maximum size of 7 mm and attains densities of 200 individuals per gram of *Z. marina* in the Chesapeake Bay (Marsh, 1976). *B. varium* was virtually eliminated from western Bay grassbeds in 1972 by Tropical Storm Agnes and has not yet recovered, even in areas where reduced grassbeds still exist (Orth, 1977 and pers. observ.). Eastern Shore *B. varium* populations did not experience as great a decline (pers. observ.) possibly due to a less severe salinity effect. The objective of this study was to preliminarily assess the quantitative and qualitative impact of grazing by *B. varium* on *Z. marina* periphyton.

METHODS AND MATERIALS

Field Work

Both live *Zostera marina* and diatom colonized polypropylene ribbon which resembled the living plants in size but was slightly paler in color were used in the grazing experiments. Living blades, collected from a Guinea Marsh *Z. marina* bed at the mouth of the York River on the southwestern shore of the Chesapeake Bay, were held for not more than two days in large wooden flow-through tanks before being used. The polypropylene strips were suspended for 30 days from a pier at the mouth of the York River to condition the blades before use. The artificial plants consisting of six 45 cm strips of ribbon tied to a wire staple were then wiped clean and anchored to the sediment in the Guinea Marsh seagrass bed to be colonized. Thirty days later the artificial grass was collected for immediate use in grazing experiments and scanning electron microscopy (SEM).

Bittium varium were collected from a *Zostera marina* bed at Vaucluse Shores on the southeastern side of the Bay. Snails were acclimated for two days in aquaria with York River water (23 °/oo salinity; 22°C) and live periphyton covered *Z. marina* prior to experimental use.

Laboratory Experiments

Periphyton-colonized artificial grass blades were used to quantitatively assess the effects of grazing. The blades that were used were initially selected based on the extent of periphyton coverage. Twenty-six blades with the densest growth were cut into 12 cm lengths. One end of each blade was then wedged against the inside of a 1/2 dram glass vial using a cheesecloth plug while the other end was tied to a piece of monofilament thread. Care was taken to keep blades moist at all times and not to disrupt the periphyton layer. The blades with vials were then suspended in two 40 liter aquaria filled with millipore filtered seawater (23 °/oo salinity). Aquaria were situated in a laboratory window with an eastern exposure and experiments were conducted under ambient light conditions. Temperatures in the laboratory fluctuated between 23° and 25°C. Each aquarium was equipped with a corner charcoal filter housing an airstone. Thirteen blades were randomly designated as experimental blades using a random numbers table and forty *Bittium varium* ($\bar{x}$ length = 2.1 mm) were placed in the vials of each. Periodic counts of the snails which crawled onto the blades were used as an indication of grazing pressure. When the experiment was terminated after 96 hours, the middle 8 cm portion of each blade (3.2 cm^2 total surface area per blade) was removed for analysis. Twelve experimental and twelve control blades were used for pigment analyses and gravimetric calculations of periphyton biomass while the remaining two blades (one experimental and one control) were prepared for SEM examination. Results of the pigment extraction and dry weight calculations were statistically analyzed using a Wilcoxin two-sample test (Sokal and Rohlf, 1969).

Chlorophyll *a* and chlorophyll degradation products (phaeopigments) were extracted from each blade and analyzed by a phase partition technique (Whitney and Darley, 1979). Three unused 8 cm long pieces of artificial grass were similarly treated and the mean absorbance values used as correction factors for solubles present in the polypropylene ribbon. Absorbance readings were measured using a Bausch and Lomb Model 21 spectrophotometer. After pigment extraction the periphyton adhering to each blade was removed by scraping with forceps, dried to a constant weight, and weighed to the nearest 0.01 mg on a Mettler balance (model H-51).

A scanning electron microscope (AMR-1000) was used to examine Bittium varium fecal pellets, grazing trails, and food selectivity on periphyton colonizing both living Zostera marina and artificial grass blades. Micrographs were also used to assess the quality and composition of the periphytic communities colonizing these substrates. When experiments were terminated, blades and fecal pellets were immediately fixed in a 3% gluteraldehyde, 0.1 M sodium cacodylate buffer (pH 7.2) and 0.25 M sucrose solution. After two hours, samples were rinsed three times for up to 30 min each in a 0.1 M buffer solution containing 0.25 M, 0.1 M and 0.0 M sucrose solutions, respectively. They were then fixed in a 1% osmium tetroxide and 0.1 M sodium cacodylate buffer (pH 7.2) for 2 to 24 hours, rinsed twice thereafter in distilled water, and dehydrated in a graded series (25, 50, 75, 90, 95 and 100%) of ethanol solutions. After dehydration, samples were critical point dried (Polaron Critical Point Drying System) with liquid CO_2, mounted on stubs and coated with gold/palladium (40:60) in a high vacuum evaporator. They were then examined and photographed under the SEM.

RESULTS

Periphyton pigment analyses of grazed and ungrazed artificial grass blades (Table 1) showed no significant differences ($p>0.05$) in chlorophyll a concentrations whereas experimental blades exhibited significantly ($p<0.001$) lower phaeophytin a concentrations than control blades. Mean chlorophyll a concentrations of 0.1882 and 0.1287 mg/l for grazed and ungrazed blades, respectively, were lower than the corresponding phaeophytin a values of 0.8607 and 1.8436 mg/l. Gravimetric differences of attached periphyton existed between grazed and ungrazed blades (significant at $p<0.001$) indicating a mean overall removal of 62.7% of the periphyton from artificial blade surfaces (Table 2).

Scanning electron micrographs (plates 1 to 24) enhanced the understanding of feeding activities by Bittium varium. Natural Zostera marina used in this study was coated with a thick layer of periphyton which spanned the width of the older blades (plate 1). At magnifications of 2200 and 4400X (plates 2 and 3) the complex nature of this crust is revealed. It consists of at least three genera of diatoms (Cocconeis scutellum, Nitzschia sp., Amphora sp.), blue-green algae, bacteria and organic debris, some of which might be degrading fecal pellets. The crust is up to 15 μm thick with as many as 3-4 layers of diatoms (plate 4).

Bittium varium ingests the periphyton crust using a taenioglossate radula consisting of seven teeth in each transverse row. The central tooth is flanked on each side by one lateral and two similar slender marginal teeth (plate 5). With the marginals laterally compressed, the radular band of an adult B. varium is approximatly 30 μm wide.

TABLE 1. PERIPHYTON PIGMENT ANALYSIS OF GRAZED AND UNGRAZED ARTIFICIAL *Z. MARINA* BLADES. SIGNIFICANT DIFFERENCES WERE DETERMINED BY THE WILCOXON TWO-SAMPLE RANK TEST(a) ($\alpha = 0.05$).

	Functional Chlorophyll A (mg/l/blade)					Phaeophyutin a (mg/l/blade)			
	Grazed		Ungrazed			Grazed		Ungrazed	
Overall Rank	1	-0.2514	3	0.0000	Overall Rank	1	0.0840	9	1.1600
	3	0.0000	3	0.0000		2	0.0988	12	1.5014
	8.5	0.0965	5	0.0322		3	0.1355	13	1.6053
	8.5	0.0965	6	0.0644		4	0.1583	14	1.6127
	8.5	0.0965	8.5	0.0965		5	0.4180	15	1.6423
	12.5	0.1609	11	0.1287		6	0.4402	17	1.8254
	16.5	0.1931	12.5	0.1609		7	0.8186	18	1.9072
	16.5	0.1931	16.5	0.1931		8	0.8756	19	2.0333
	16.5	0.1931	16.5	0.1931		10	1.1848	20	2.0977
	21.5	0.2574	16.5	0.1931		11	1.4026	21	2.1025
	23	0.2896	20	0.2252		16	1.7637	22	2.1816
	24	0.9332	21.5	0.2574		24	2.9488	23	2.4539
	n =	12		12			12		12
	$\bar{X}$ =	0.1882		0.1287			0.8607		1.8436
	s.d. =	0.2738		0.0889			0.8609		0.3560
	CV(b) =	145%		69%			100%		19%
	U(c) =		82 ns					125***	

(a) ns = not significant at P = 0.05

*** = significant at $P \leq 0.001$

(b) CV = coefficient of variation

(c) U = Mann-Whitney U test statistic

TABLE 2. GRAVIMETRIC ANALYSIS OF PERIPHYTON (DRY WEIGHT) ON GRAZED AND UNGRAZED ARTIFICIAL Z. MARINA BLADES AFTER 96 HR. SIGNIFICANT DIFFERENCES WERE DETERMINED BY HE WILCOXON TWO-SAMPLE RANK TEST ($\alpha = 0.05$).

Overall Rank	g. periphyton/ g. art. Zostera	mg. periphyton/ cm^2 blade	Overall Rank	g. periphyton/ g. art. Zostera	mg. periphyton/ cm^2 blade	$\bar{x}$ number B. varium grazing/hr/blade
1	0.79	0.124	12	0.44	0.069	32.8
2	0.75	0.118	14	0.40	0.063	34.1
3	0.71	0.112	15	0.35	0.055	26.6
4	0.66	0.103	16	0.32	0.050	25.0
5.5	0.62	0.098	17	0.31	0.049	27.3
5.5	0.62	0.098	18	0.26	0.041	26.2
7	0.59	0.093	19	0.18	0.028	25.8
8	0.56	0.088	20	0.15	0.024	28.5
9	0.50	0.079	21	0.09	0.014	35.6
10	0.48	0.076	22.5	0.08	0.013	29.2
11	0.47	0.074	22.5	0.08	0.013	33.1
13	0.42	0.066	24	0.06	0.009	32.6
n =	12	12		12	12	12
$\bar{X}$ =	0.59	0.094		0.22	0.035	29.73
s.d. =	0.12	0.018		0.14	0.021	3.70
CV$^{(a)}$=	19.8%	19.1%		62.1%	.6%	12.4%
U$^{(b)}$=	143***					

Oberall periphyton reduction = 62.7%

*** = significant at $p \leq 0.001$

(a) CV = coefficent of variation

(b) U = Mann-Whitney U test statistic

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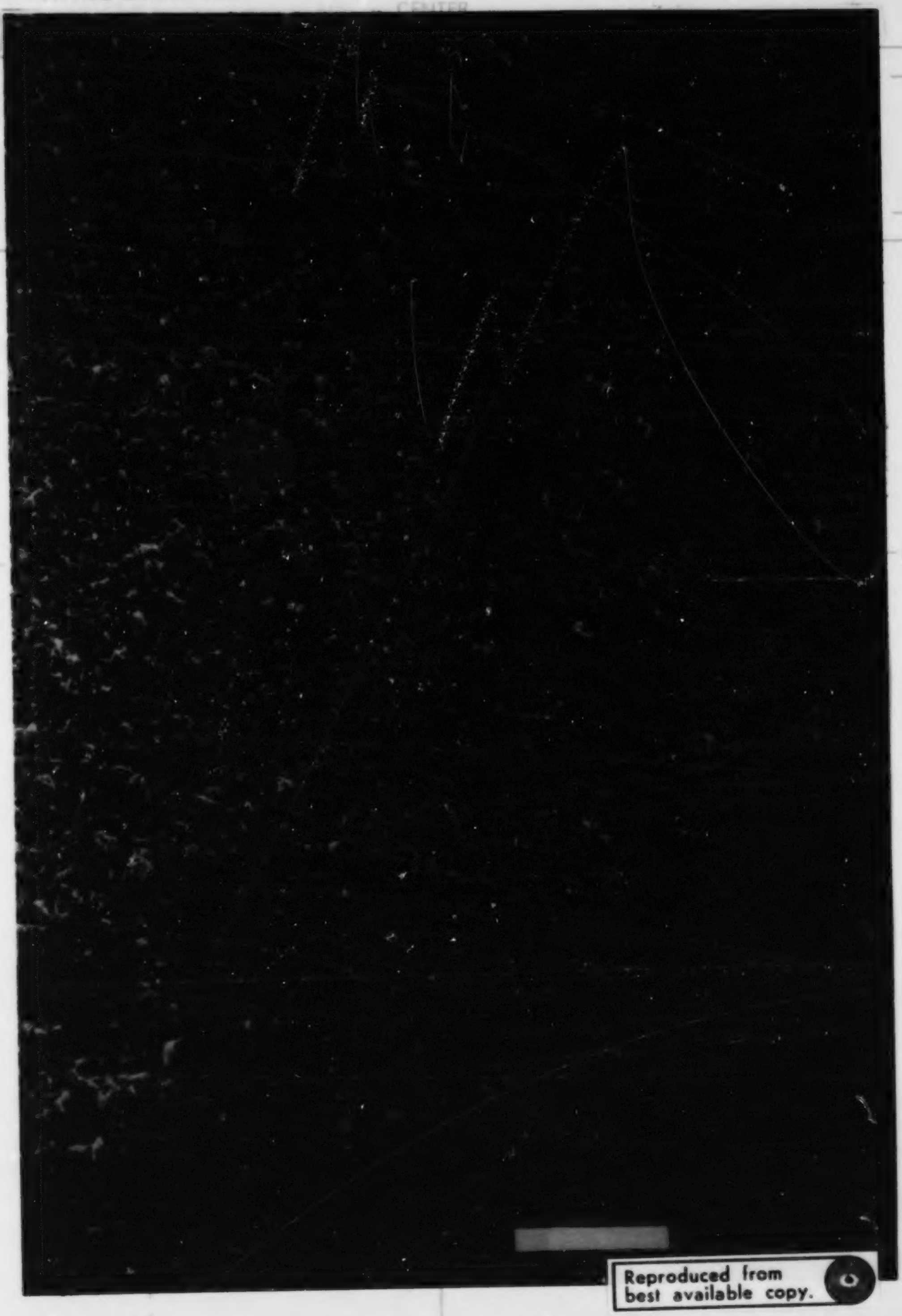

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Plate 1. Live Zostera marina showing complete coverage by the periphyton crust (260X; size bar = 100 μm).

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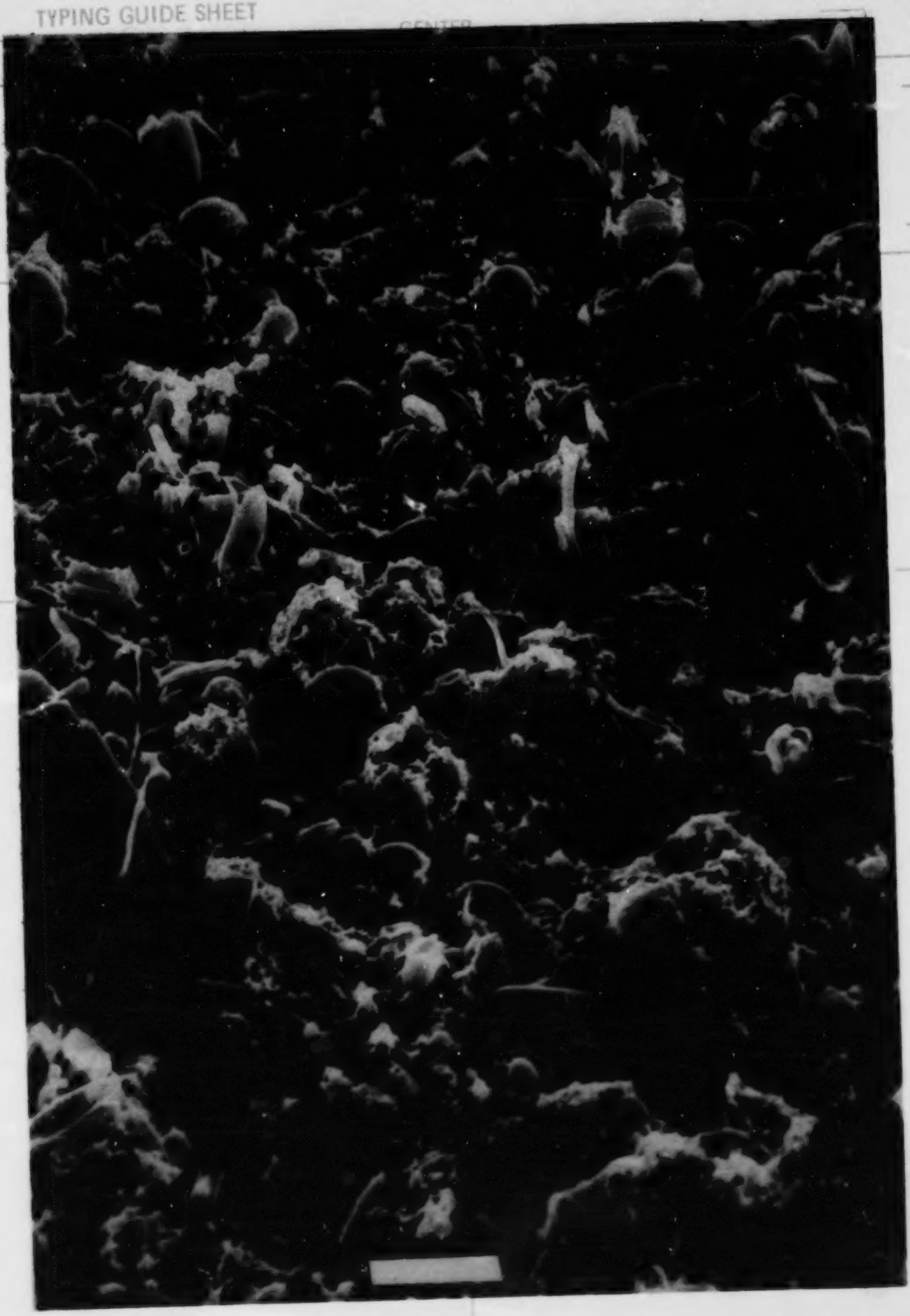

Plate 2. Detail of plate 1 showing organic debris and at least three species of diatoms including *Cocconeis scutellum*, *Amphora* sp. and possibly *Nitzschia* sp. (2200X; size bar = 10 μm).

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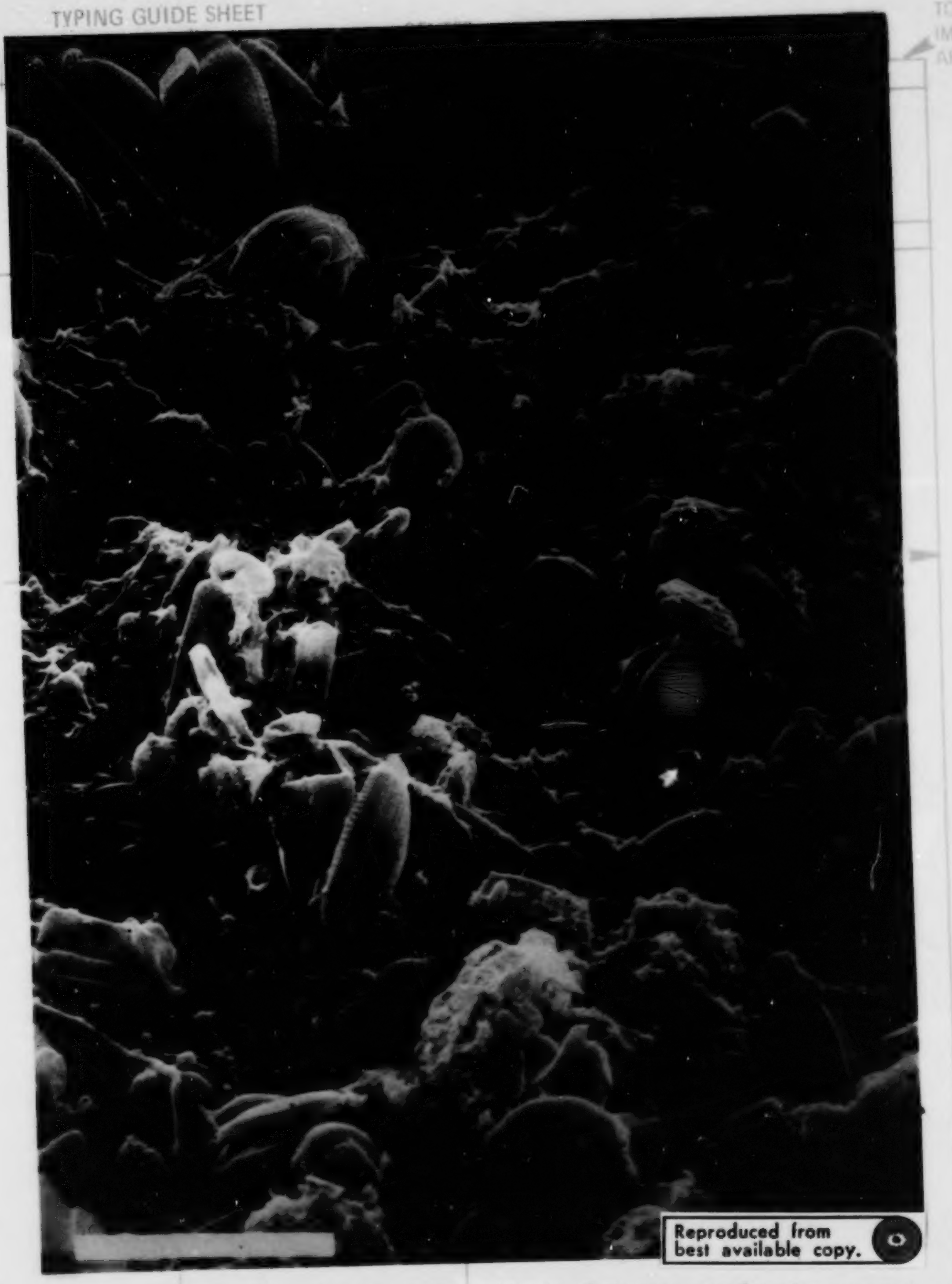

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Plate 3. Part of a live Zostera marina blade that was completely covered with periphyton revealing the complex nature of the crust. The periphyton community included blue-green algae, diatoms, bacteria and organic debris, embedded in a mucous matrix (4400X; size bar = 10 µm).

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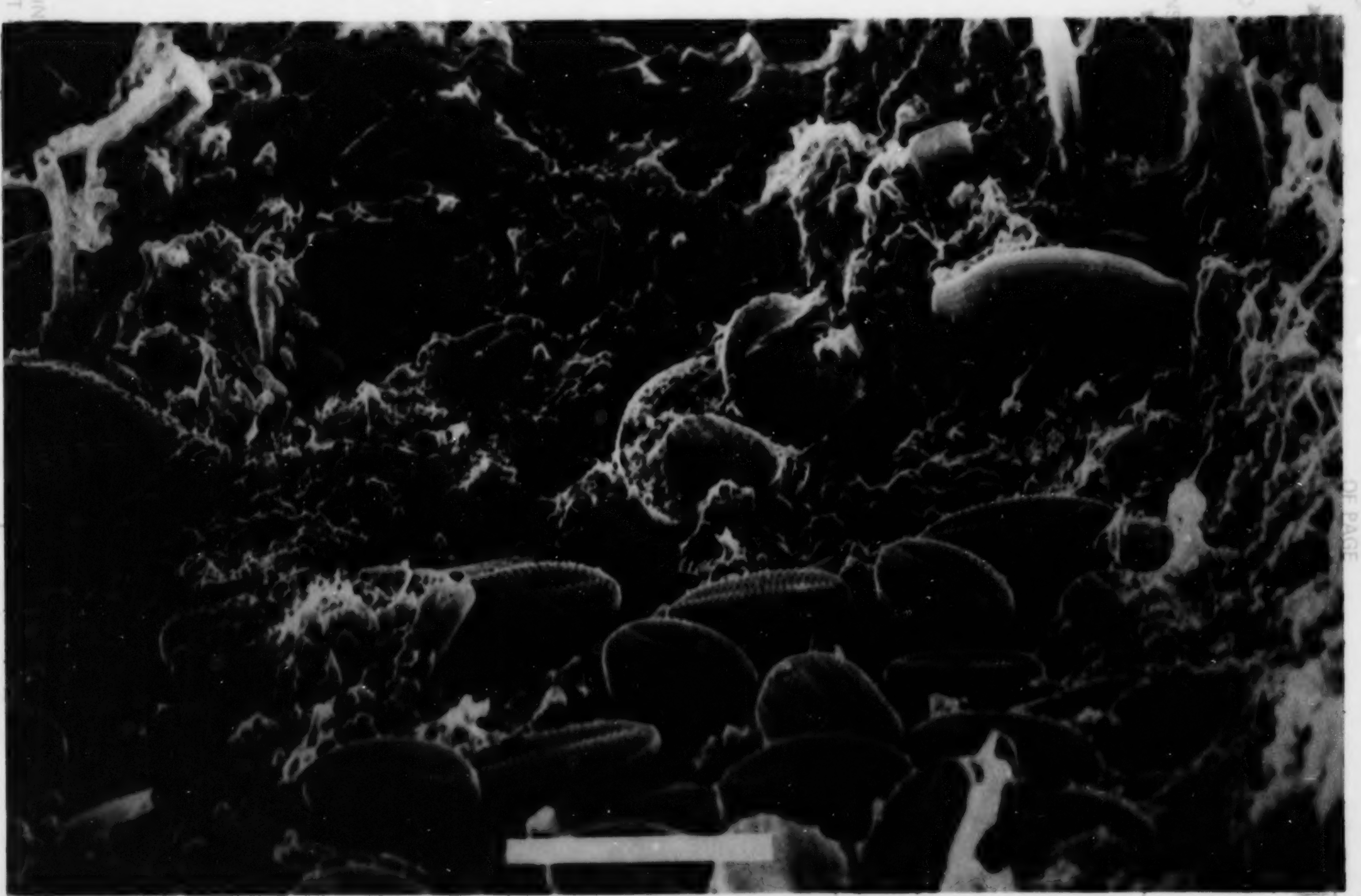

Plate 4. The thickness of the periphyton crust is shown with *Cocconeis scutellum* and bacteria adhering directly to *Zostera marina* epithelium and other pennate diatoms, blue-green algae, bacteria and organic debris incorporated in the upper portions (4400X; size bar = 10 µm).

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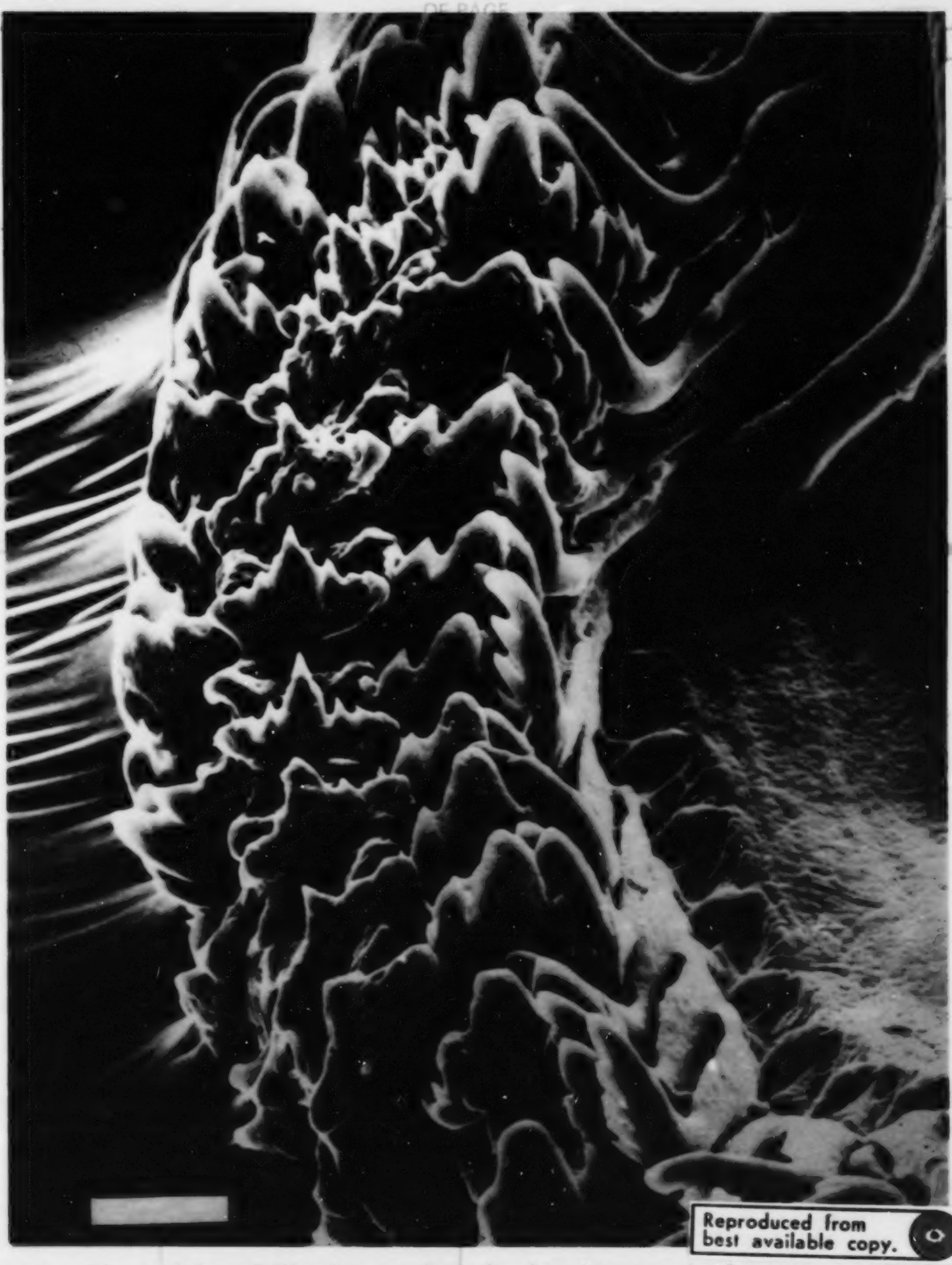

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Plate 5. The radula of Bittium varium showing its taenioglossate configuration with one central tooth flanked by a lateral and two marginal teeth on each side. Note that the central teeth are badly worn in some cases. The width of the radula is approximately 30µm with the marginal teeth laterally compressed (2200X; size bar = 10 µm).

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Grazing by *Bittium varium* on periphyton of live *Zostera marina* results in various effects (plates 6 to 8). Some feeding activities remove the upper layer of periphyton crust, with little damage to the underlying diatoms (plates 6 to 9). In most cases, grazed patches occur in which the total periphyton matrix is removed, leaving only a few bacteria attached to the *Z. marina* epithelium (plates 10 to 12). Distinct grazing trails are evident in other micrographs (plates 13 to 15). Individual straight-run trails vary in width from approximately 19 to 29 µm (plates 13 and 14). Impressions of *Cocconeis scutellum* in the *Z. marina* epithelium indicate that this tightly adhering species is sometimes removed by *B. varium* (plates 14 and 15). However, examinations of fecal pellets (plate 16) reveal that pennate diatoms such as *Nitzschia* and *Amphora* are commonly ingested, suggesting that these species are less tightly adhered to the grass blades. Closer examination of the diatom frustules observed in this fecal pellet revealed the absence of protoplasm that fills the pores in live diatoms which is evidence that they are digested as well (plates 17 and 18).

The periphyton assemblage found on polypropylene ribbon (plates 19 to 21) is very different from that of living *Zostera marina*. A hair-like mat of unidentified tubular material (possibly diatom sheaths and bacterial filaments) and organic debris covers the entire blade. The virtually complete removal of the hair-like mat after grazing (plate 22) revealed patches of pennate diatoms that were evident under higher magnification (plates 23 and 24). The considerable reduction in periphyton biomass as a result of grazing by *Bittium varium*, evidenced in the gravimetric data (Table 2), is readily apparent in micrographs of grazed artificial blades.

DISCUSSION

Grazing on periphyton of marine macrophytes may have important implications for the productivity, distribution and abundance of the colonized plants. *Zostera marina* has experienced widespread declines primarily on the western shore and, to a lesser extent, the eastern boundary of the Chesapeake Bay (Orth et al., 1979). Reasons for the observed declines are as yet unclear but factors such as climatological changes, herbicides, increased turbidity and increased nutrient loading have been hypothesized. Epiphytic growth has been cited as the major causative factor in similar historical declines of freshwater macrophytes of eutrophic lakes (Phillips et al., 1978; Moss, 1979). The macrophyte host is adversely affected by epiphytes since the latter absorb much of the light that normally reaches the plant surface and also act as a barrier to carbon uptake (Sand-Jensen, 1977). Epiphytic fouling, if rapid and severe enough, can eventually kill the host plant.

Two mechanisms to control colonization on marine plants by epiphytes have evolved. Many plants produce mucous or periphyton inhibiting substances (Cariello and Zanetti, 1979; Zapata and McMillan, 1979) while others, such as *Zostera marina*, vegetatively generate clean, actively photosynthetic tissue at a rapid rate while sloughing off fouled blades (Sand-Jensen, 1977). If conditions such as nutrient enrichment (abiotic) and/or the reduction or elimination of grazers (biotic) enhance periphyton growth, the formation of new photosynthetic tissue may be too slow for the continued health and survival of the macrophyte. Thus, the micrograzer component of seagrass

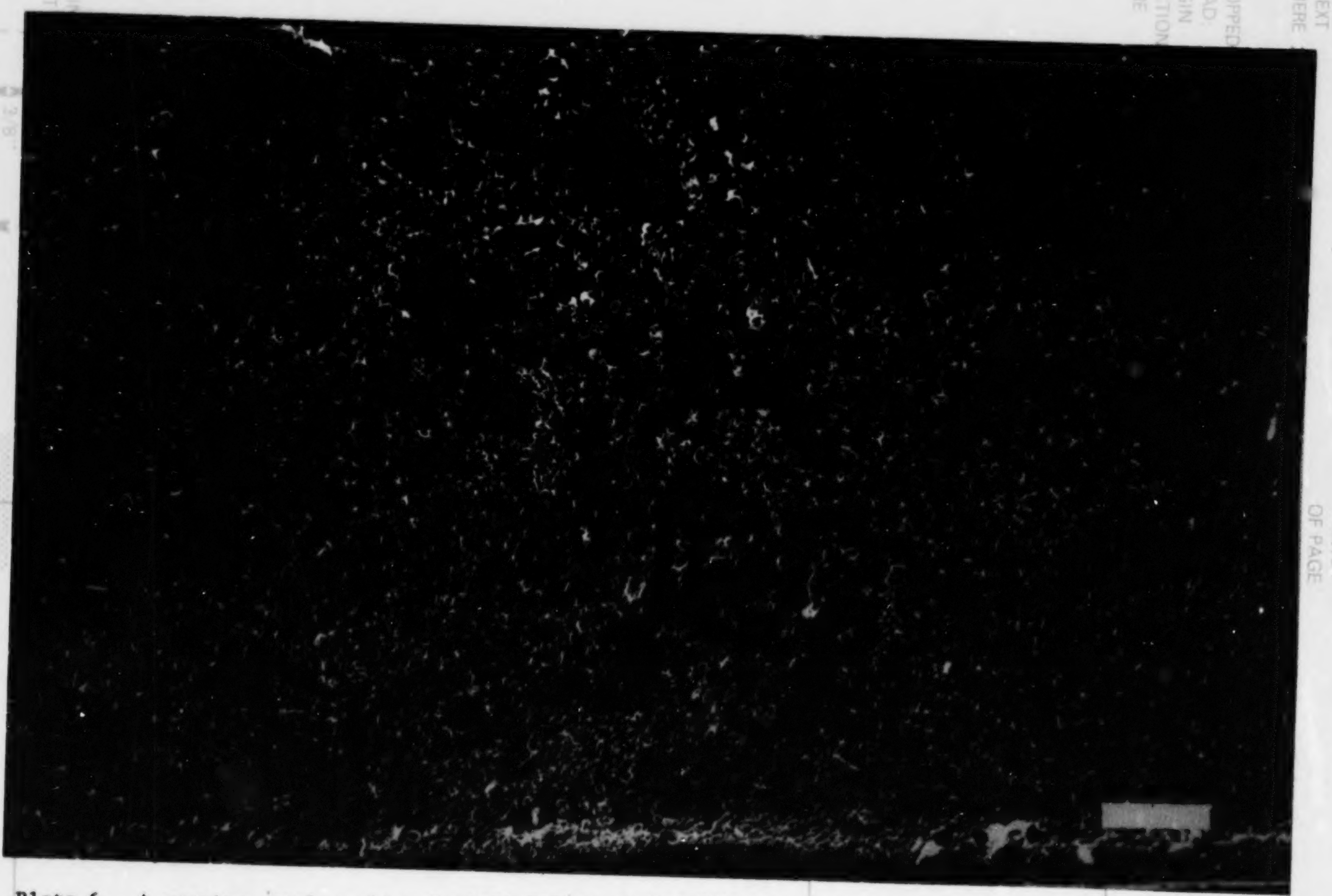

Plate 6. A grazing patch on live *Zostera marina* produced by several *Bittium varium*. Note the faint outline of *Z. marina* cells beneath the periphyton crust in the grazed areas (180X; size bar = 100 µm).

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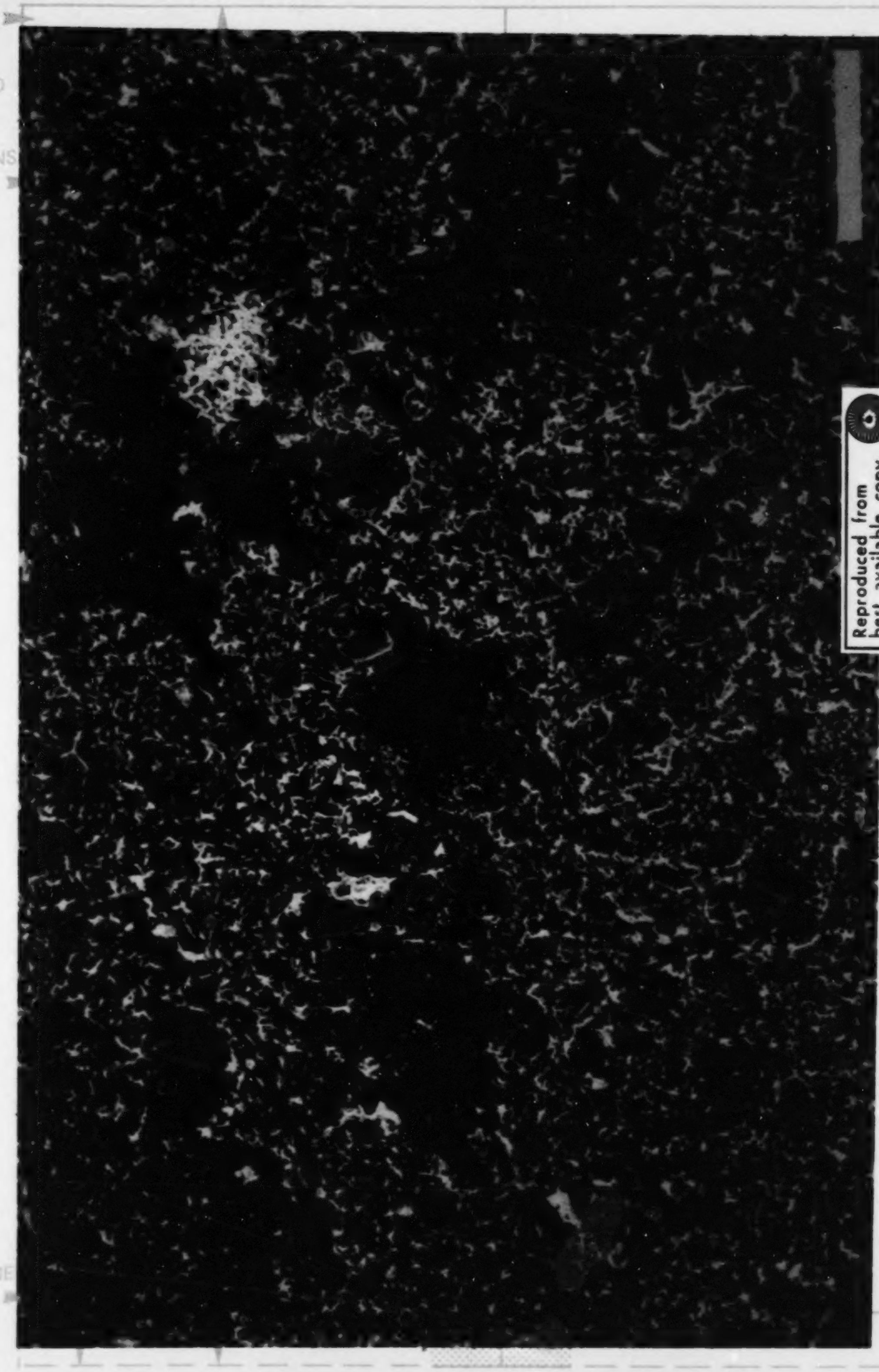

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Plate 7. A grazed patch showing the removal of the upper half of the periphyton crust (330X; size bar = 100 μm).

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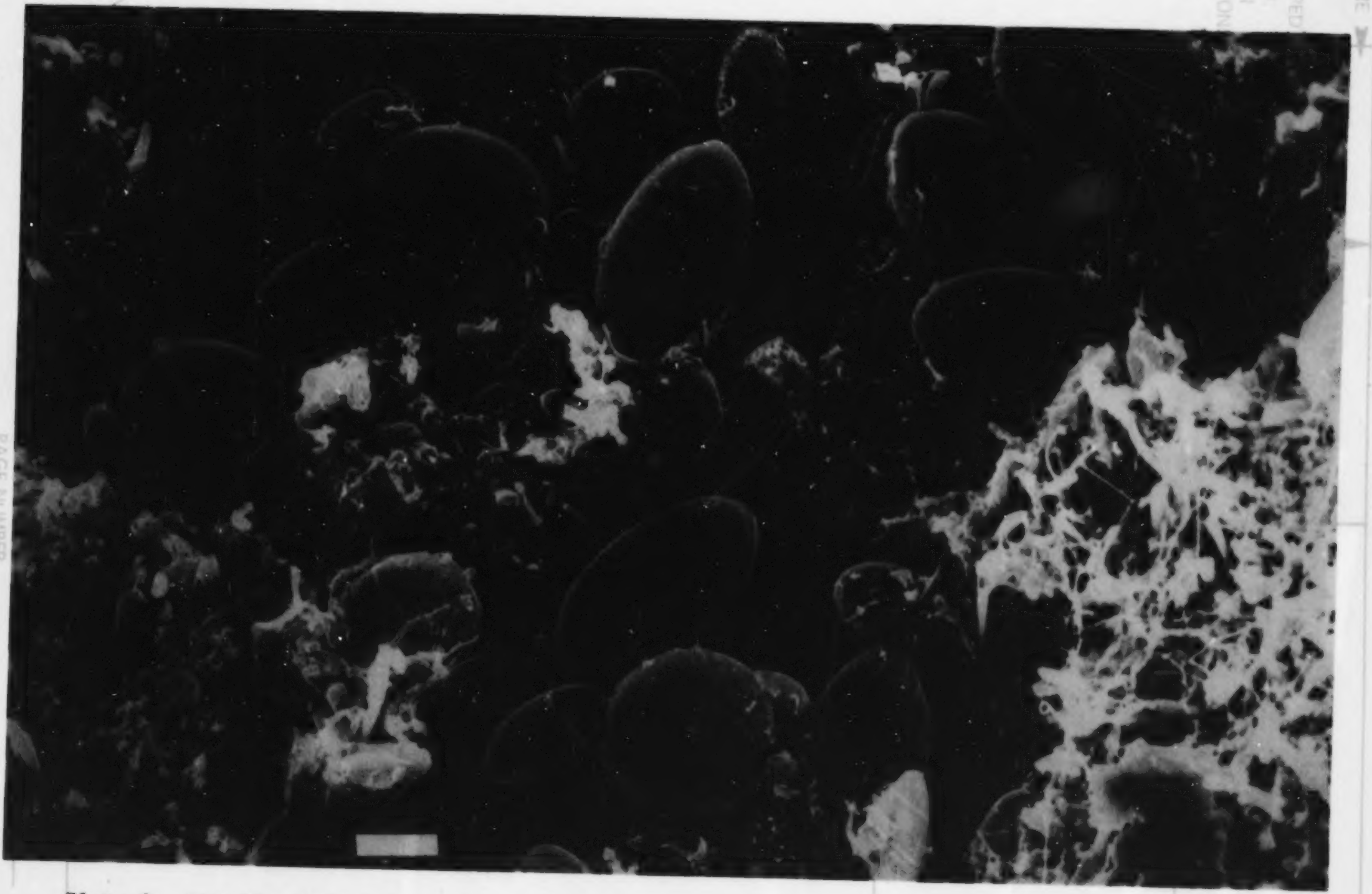

Plate 8. Detail of plate 7. Note the damage to some underlying Cocconeis scutellum after grazing although the majority are still intact and attached to the Zostera marina epithelium (750X; size bar = 100 μm).

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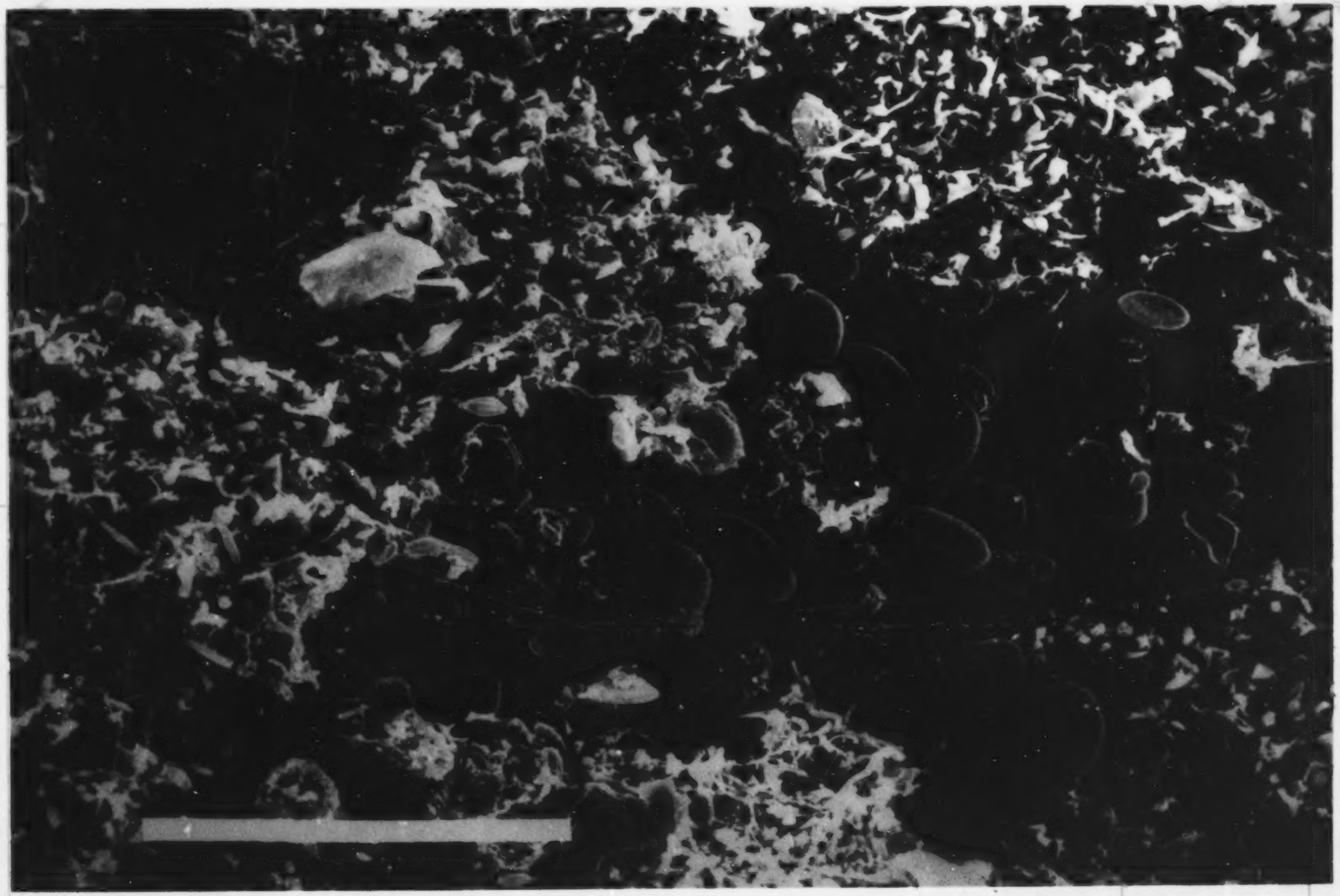

Plate 9. Detail of plate 8. The majority of slender pennate diatoms (*Amphora* and *Nitzschia*) were consumed. Some *Cocconeis scutellum* pictured show the lower half of the frustule still attached to the *Zostera marina* blade and may represent prior damage. Grazing damage to several *C. scutellum* evident in the form of cracks or holes in the frustules while they still remain attached to the blade (1300X; size bar = 10 μm).

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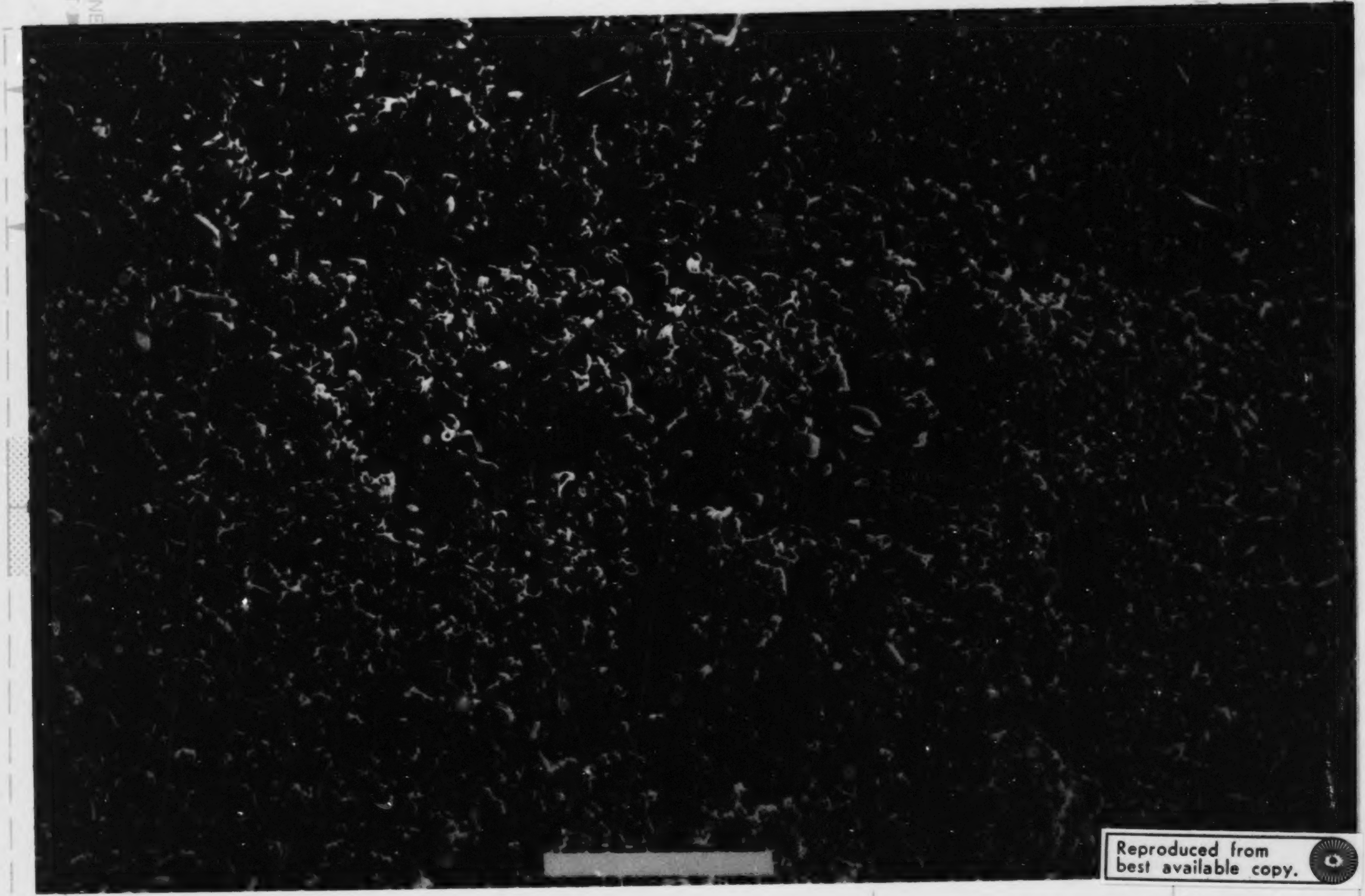

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Plate 10. A grazed region showing the almost complete removal of encrusting periphyton (390X; size bar = 100 µm).

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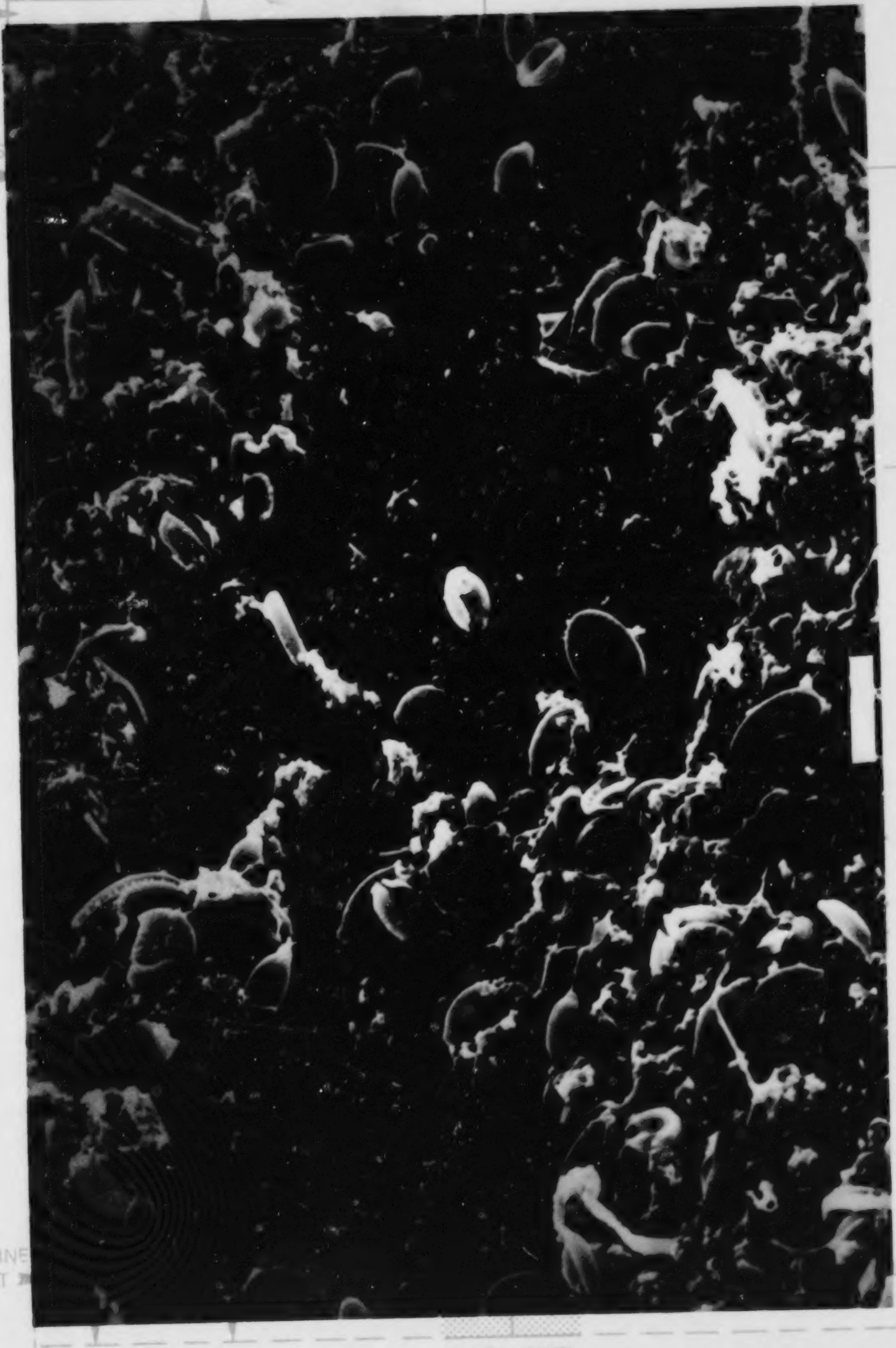

Plate 11. Enlargement of plate 10. The periphyton crust has been ingested exposing the underlying *Zostera marina* cells (1700X; size bar = 10 μm).

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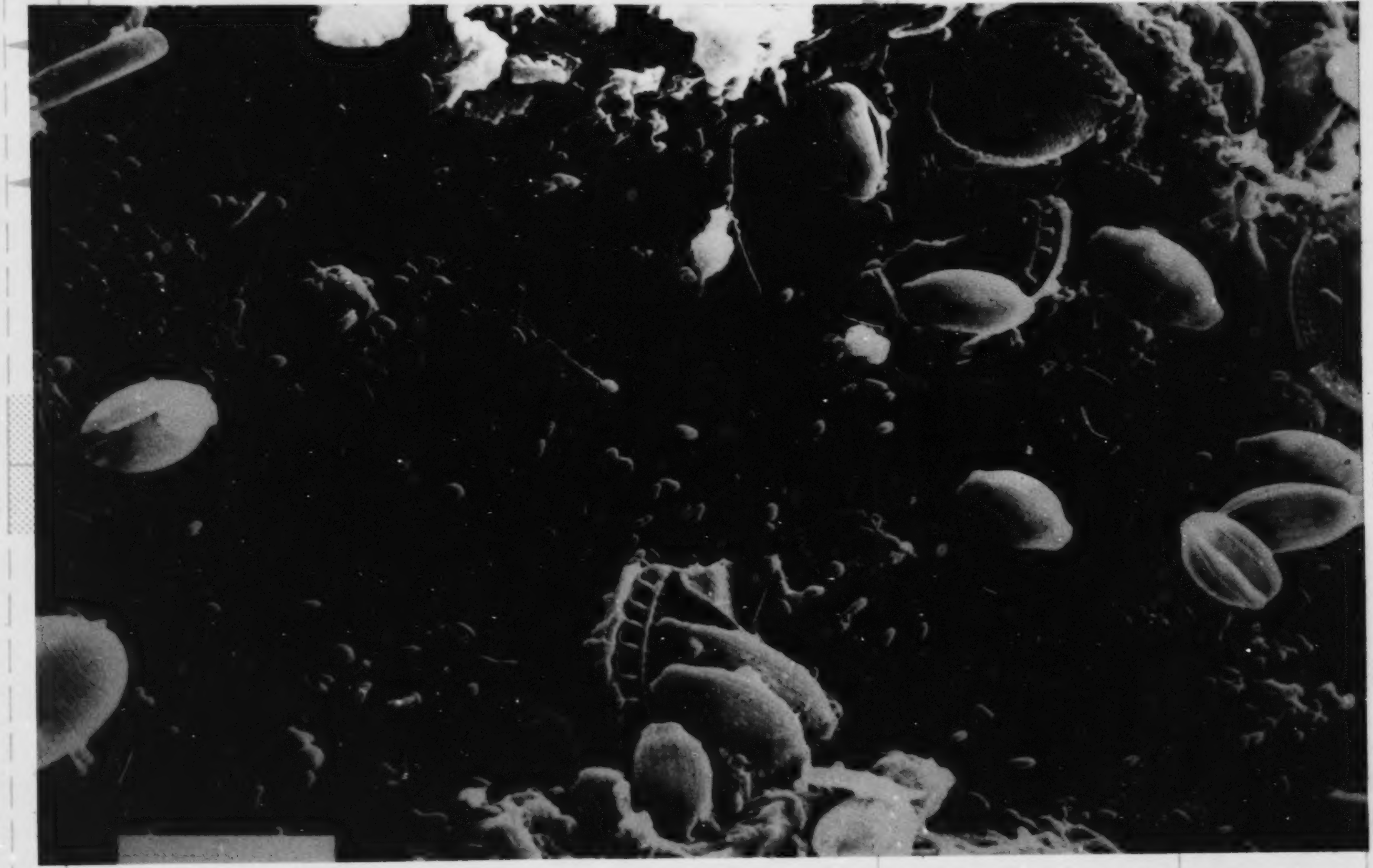

Plate 12. Enlargement of plate 11. Only a few diatoms remain within the grazing trail and some show evidence of damage. Numerous bacteria are still attached to the "cobblestone" pavement of *Zostera marina* cells (3700X; size bar = 10 μm).

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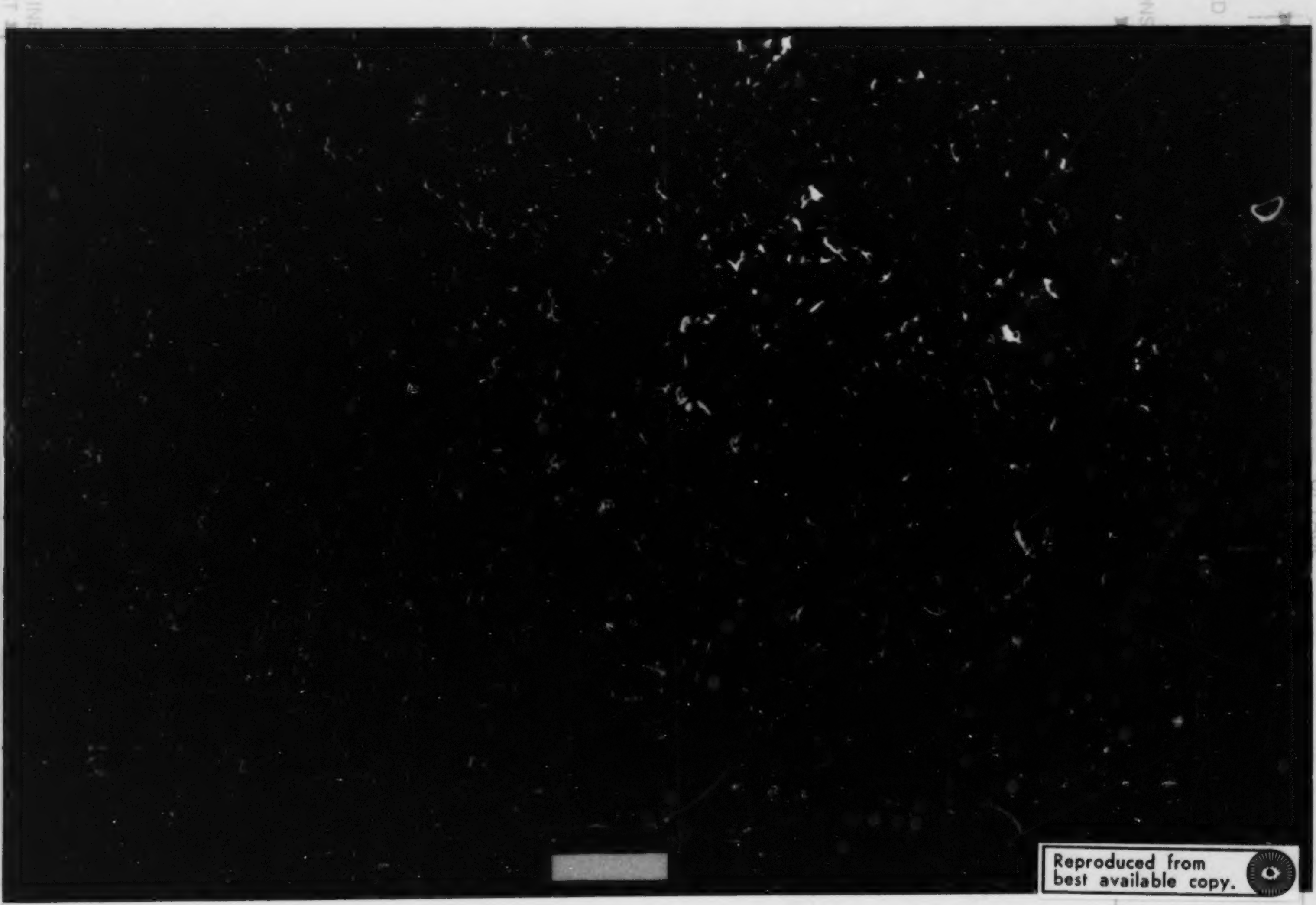

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Plate 13. The effects of grazing by 10 Bittium varium are apparent in this micrograph. Several individual trails measuring approximately 20-30μm can be seen. The live Zostera marina blade was cut longitudinally into a 1 mm wide strip prior to exposing the blade to grazers so that their feeding area was restricted. Snails were allowed to graze for approximately 2 hours (200X; size bar = 100 μm).

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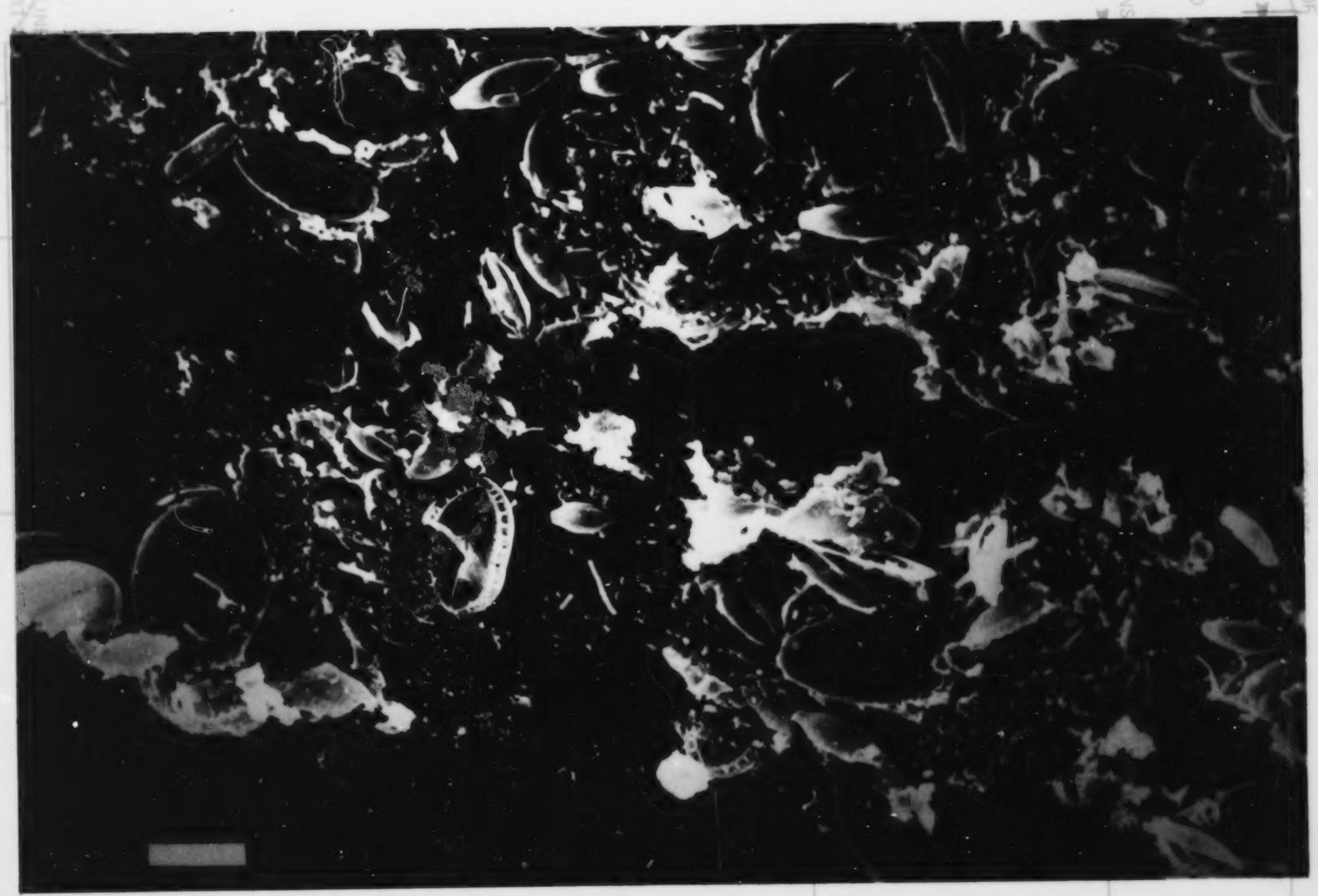

Plate 14. Enlargement of plate 13 showing an individual grazing trail. Note the impressions in the Zostera marina epithelium left by several Cocconeis scutellum (1500X; size bar = 10 μm).

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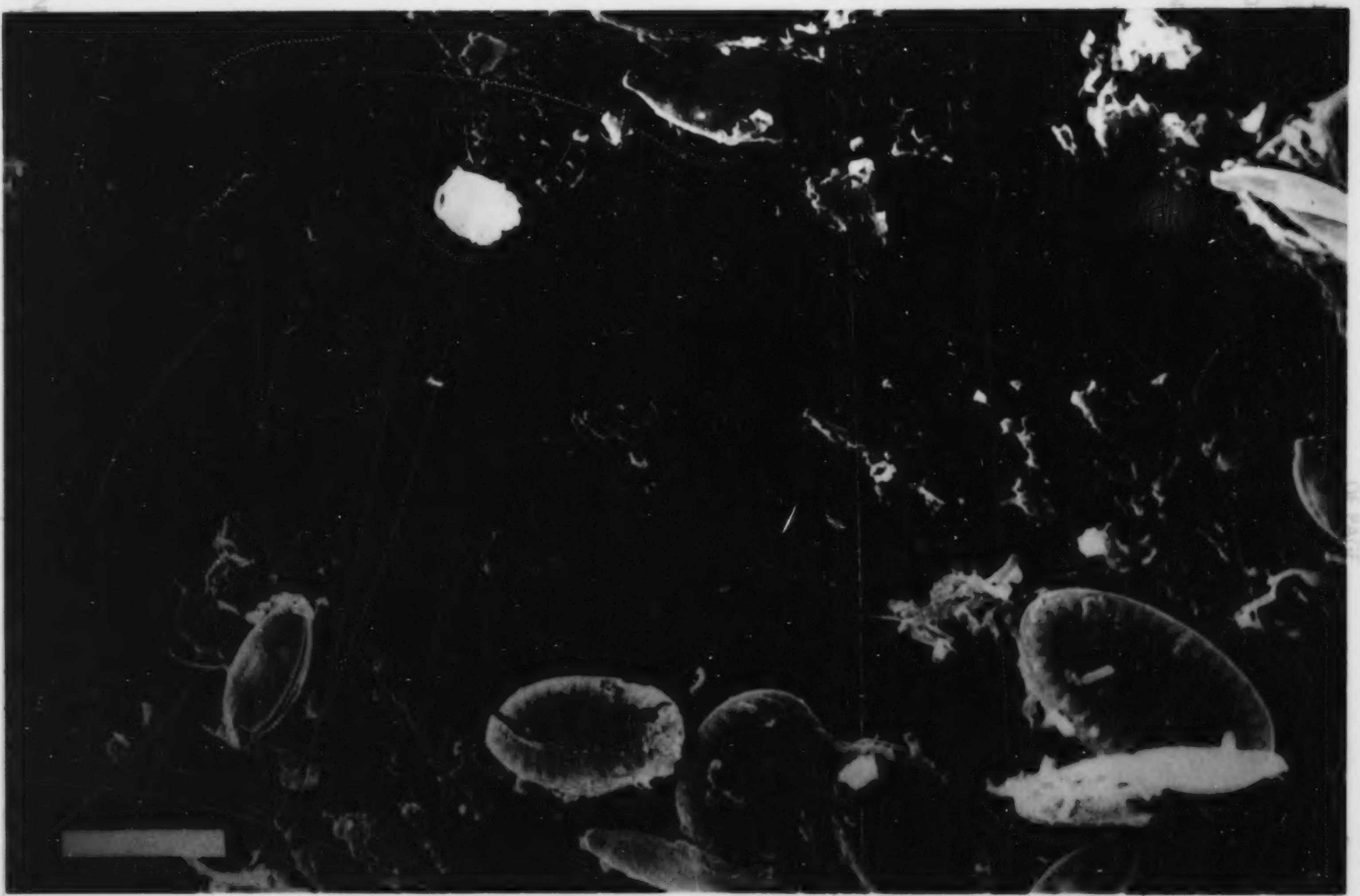

Plate 15. Enlargement of the second upper trail in Plate 13 (use circular white speck for orientation - see arrow). Impressions of Cocconeis scutellum in the grazed portion are evident as are three damaged frustules (2600X; size bar = 10 μm).

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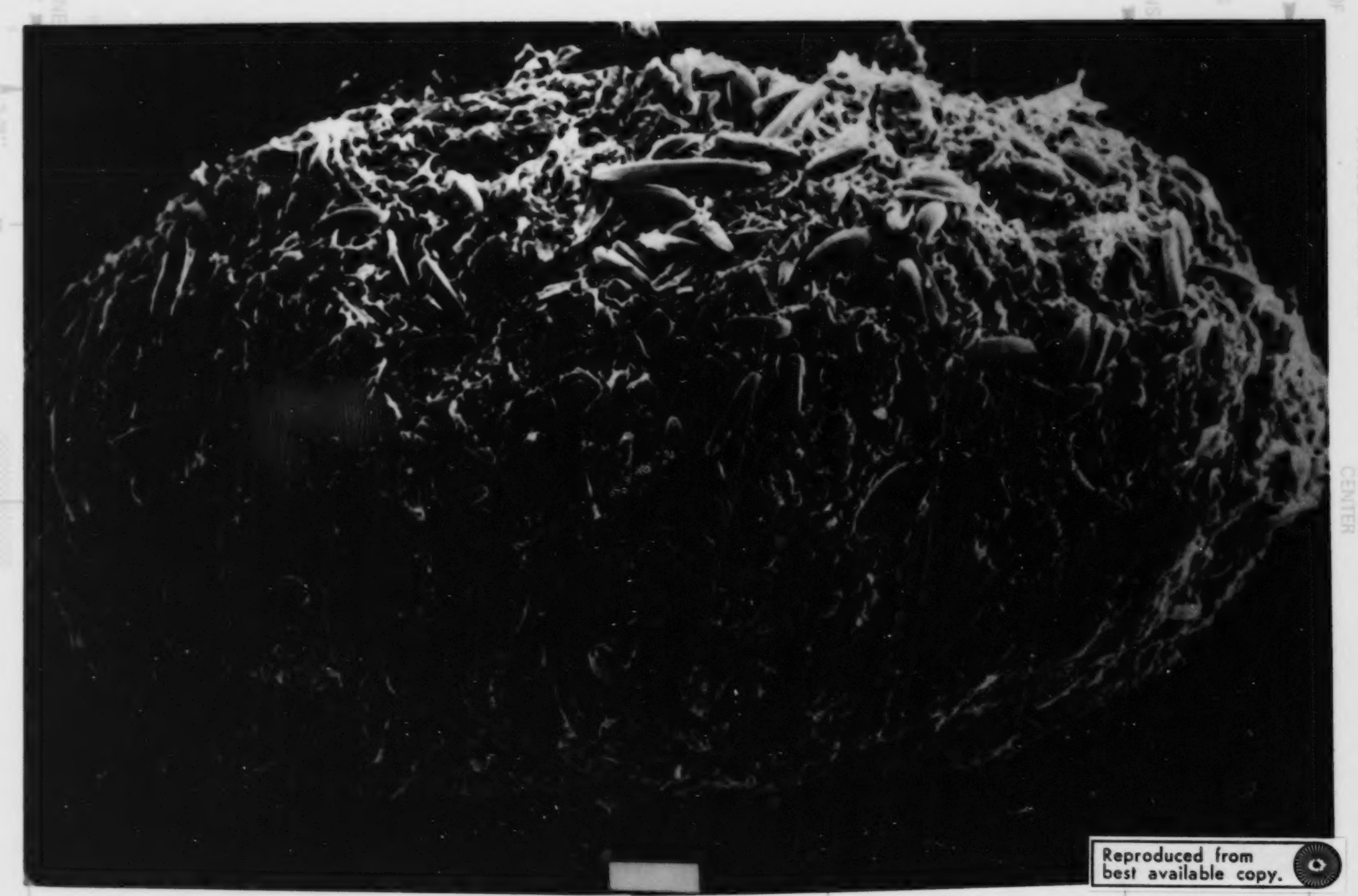

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Plate 16. _Bittium varium_ fecal pellet showing several inorganic (possibly sediment) particles and numerous diatoms, most of which are elongate forms (i.e., _Amphora_ and _Nitzschia_) like those found in the upper part of the periphyton crust. Only a single _Cocconeis scutellum_ (see arrow) is visible (1500X; size bar = 10 µm).

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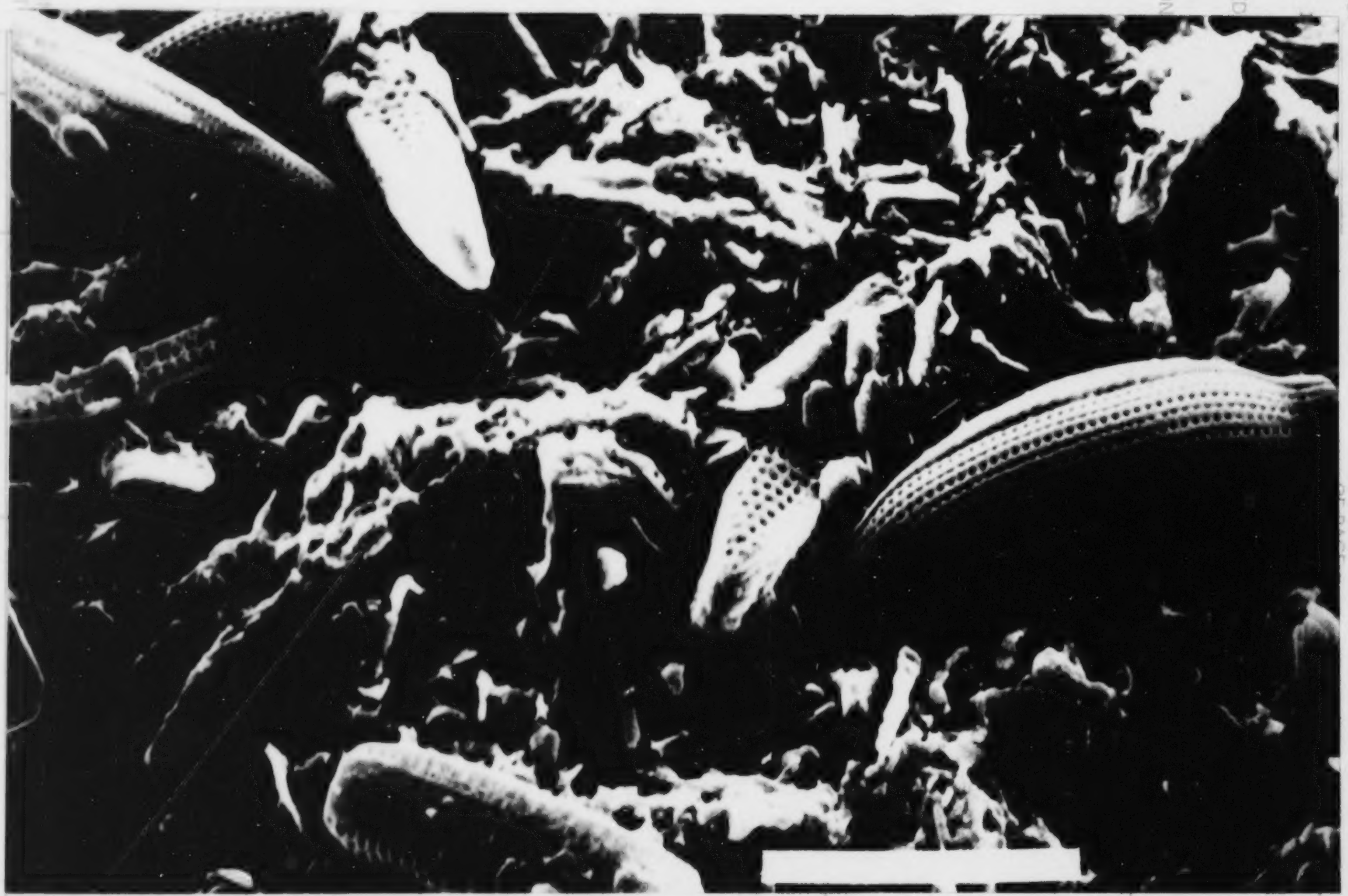

Plate 17. Enlargement of plate 16 showing three species of diatoms (Amphora sp., Nitzschia sp. and one unidentified) in the fecal pellet. Note the absence of protoplasm in the diatom pores indicating that these species are also digested as well as ingested (11,000X; size bar = 5 µm).

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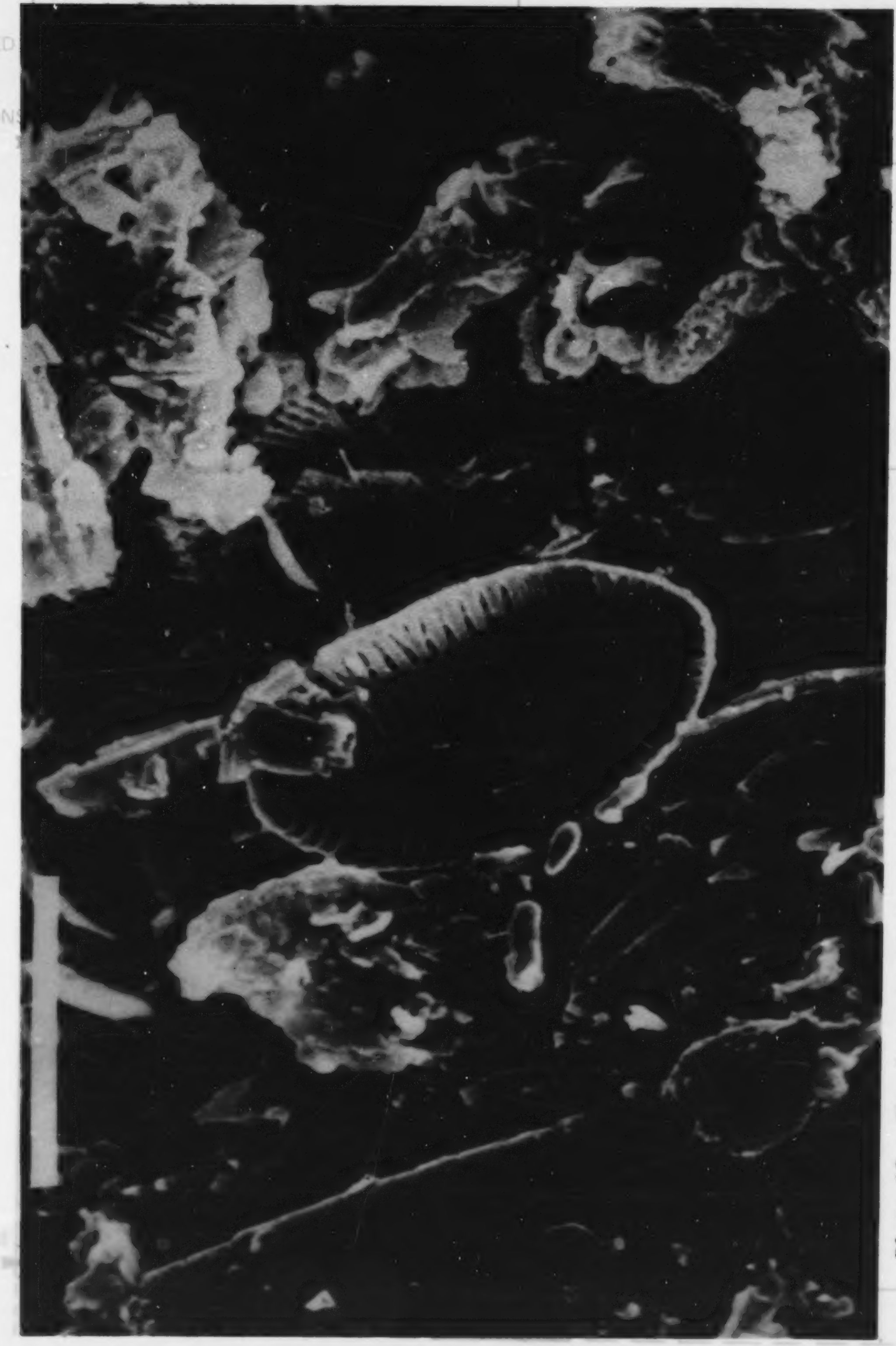

Plate 18. The frustule of the *Cocconeis scutellum* seen in plate 16 also indicates that its protoplasm was digested (11,000X; size bar = 5 µm).

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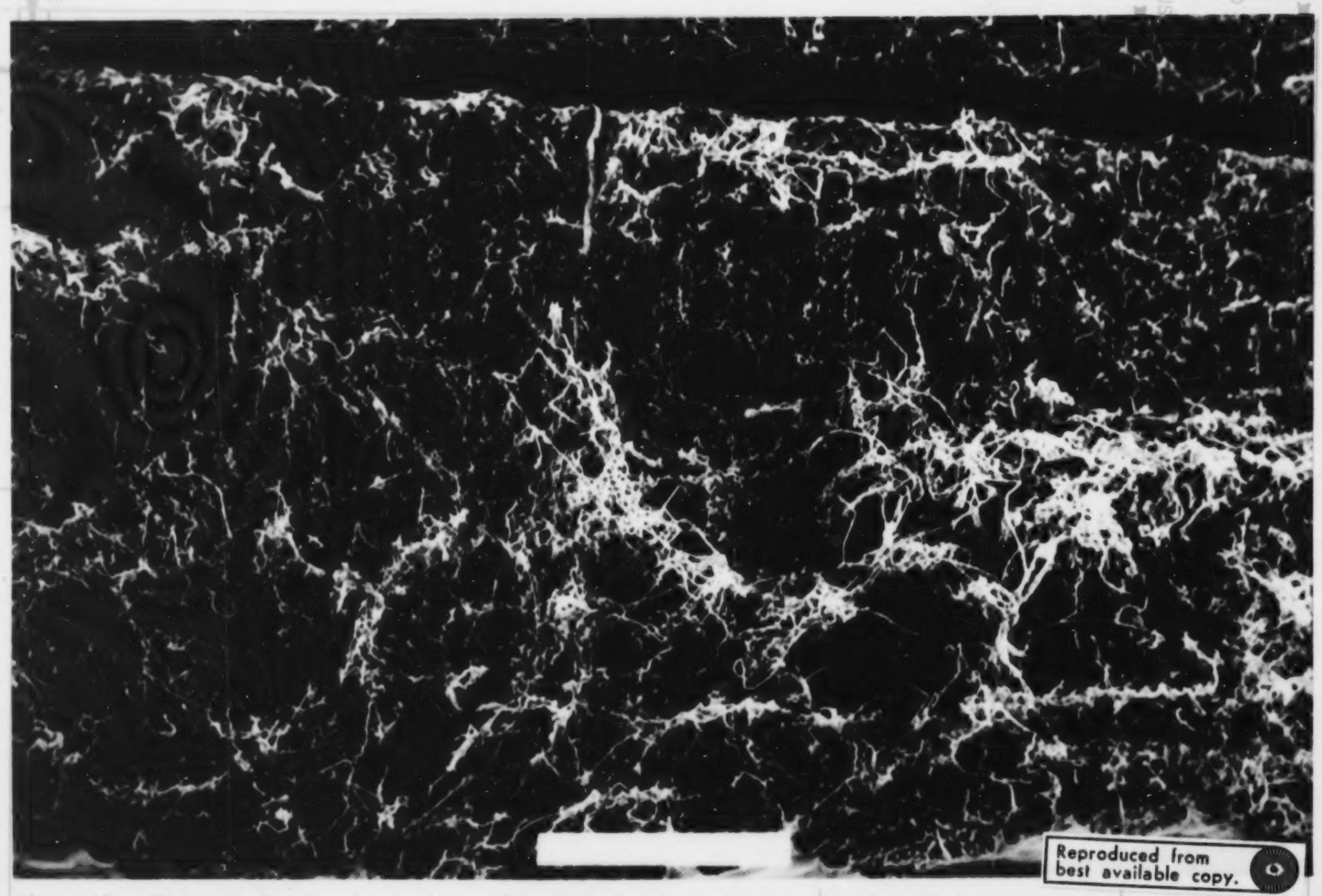

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Plate 19. Micrograph of colonized artificial Zostera marina showing hair-like mat of diatom sheaths and filamentous bacteria covering the blade (40X; size bar = 1000 μm).

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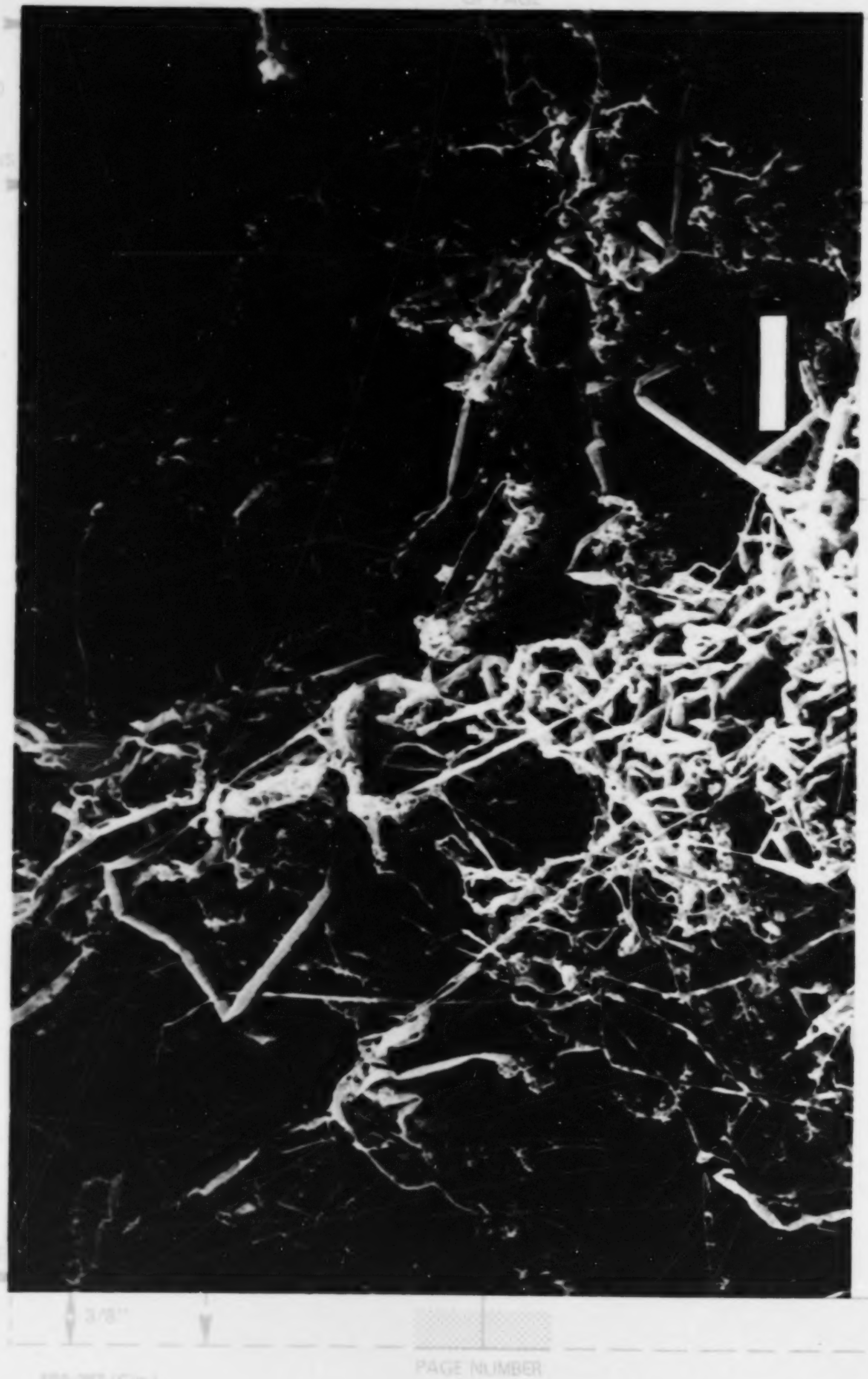

Plate 20. Detail of plate 19 showing the incorporation of some organic debris (220X; size bar = 100 µm).

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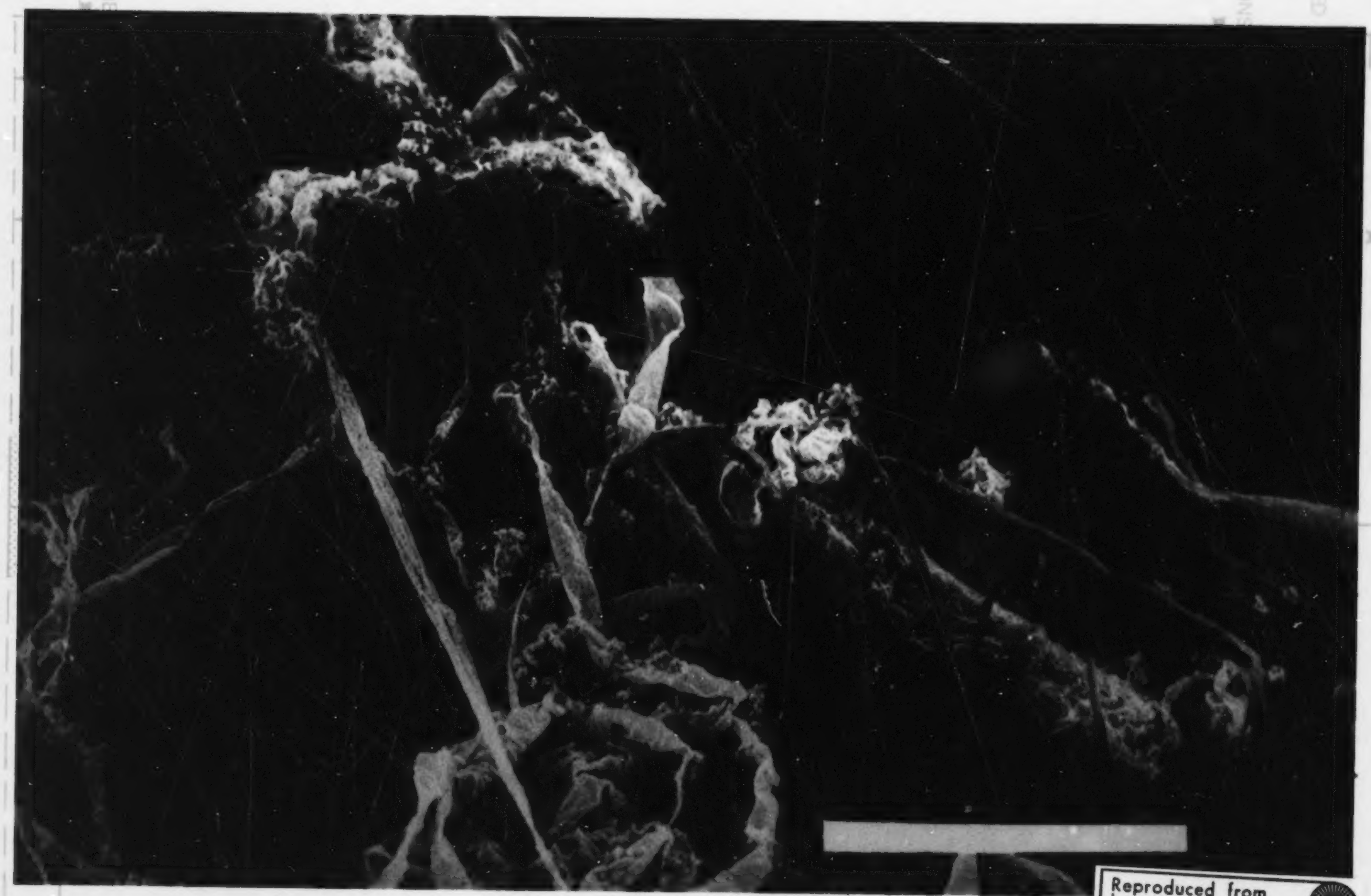

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Plate 21. Enlargement of plate 20 (650X; size bar = 100 μm).

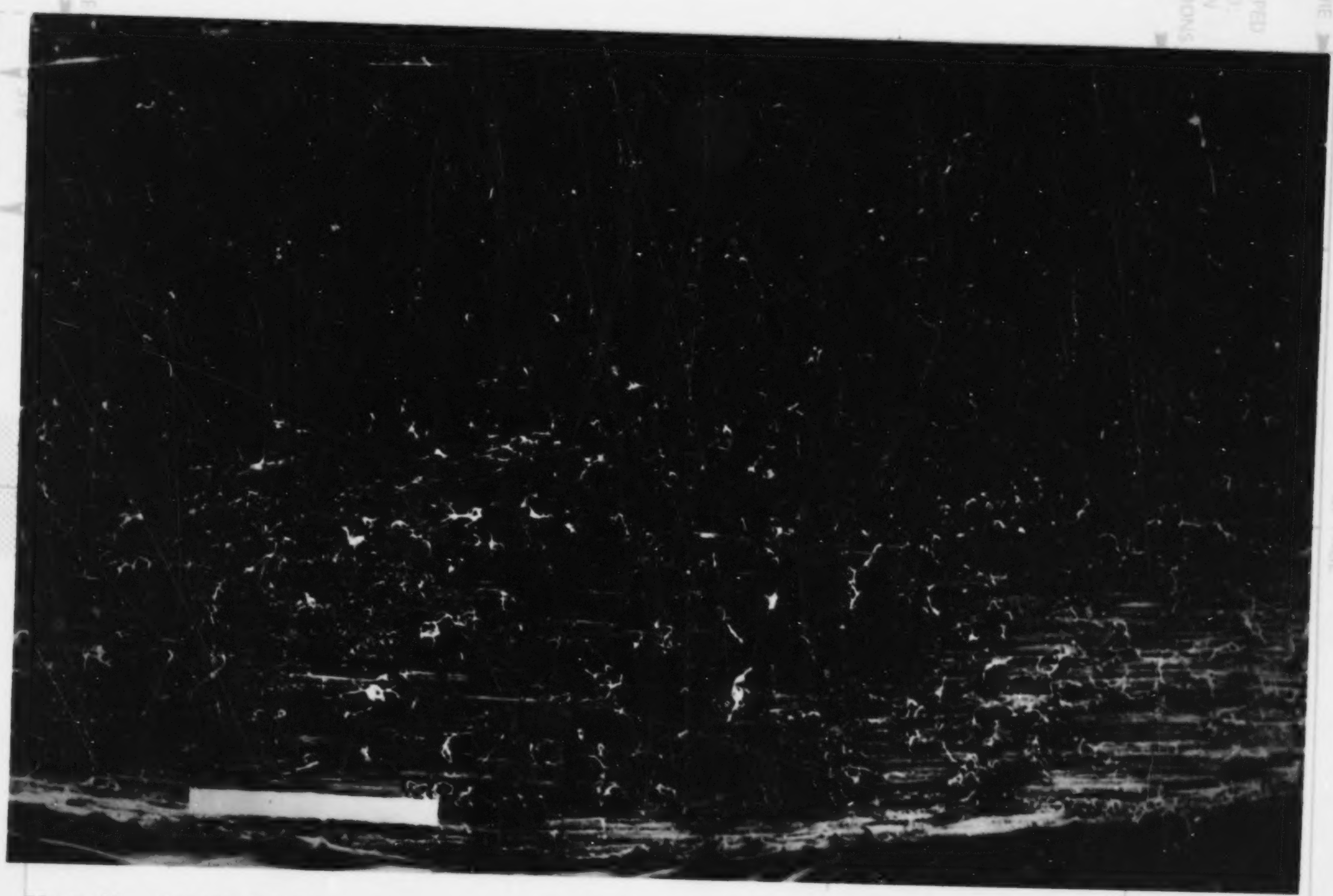

Plate 22. Artificial _Zostera marina_ blade after grazing by 30 _Bittium varium_. This blade originally resembled the one in Plate 8 (40X; size bar = 1000 μm).

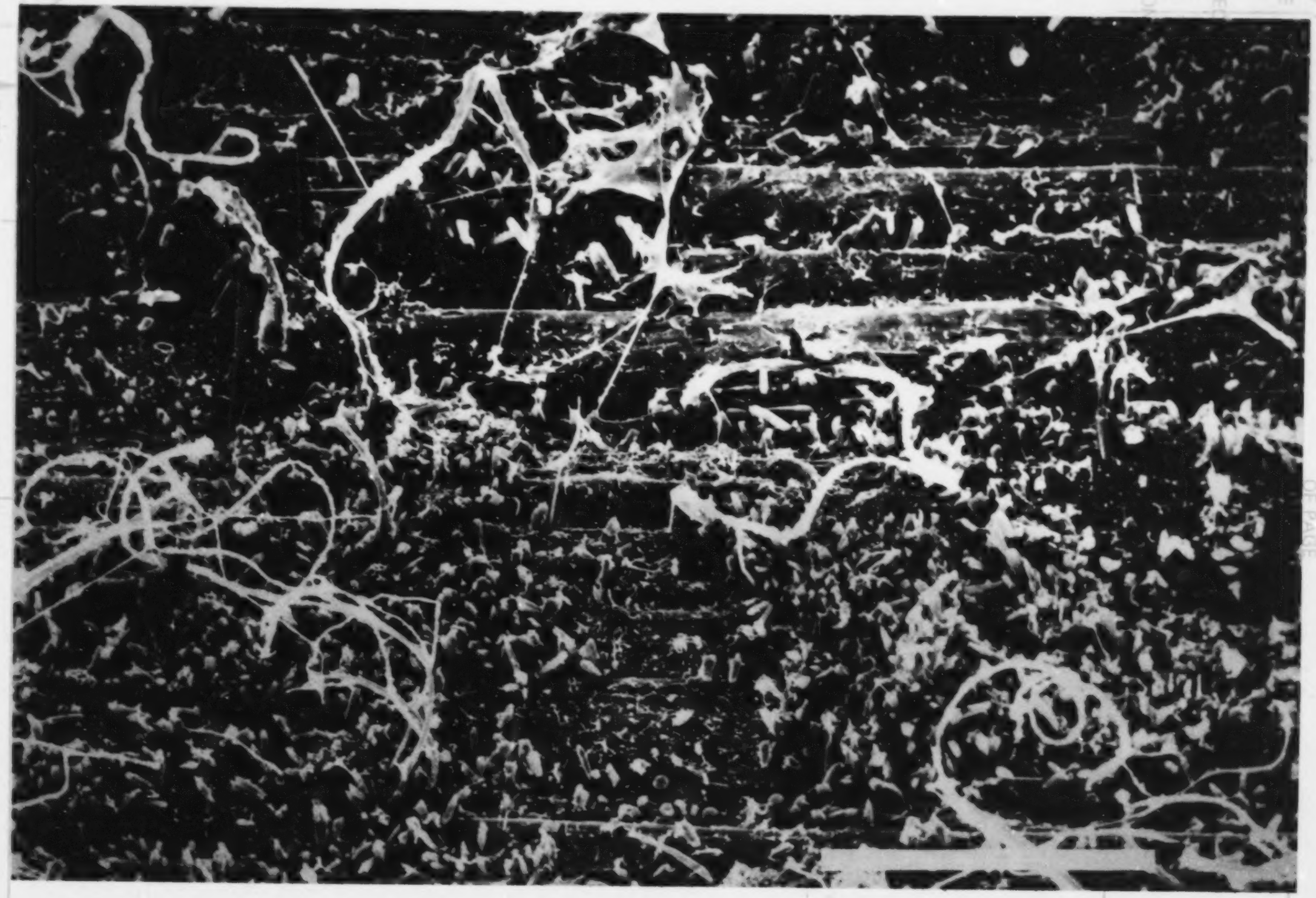

Plate 23. Enlargement of plate 22 showing the presence of numerous pennate diatoms below the hair-like mat (600X; size bar = 100 μm).

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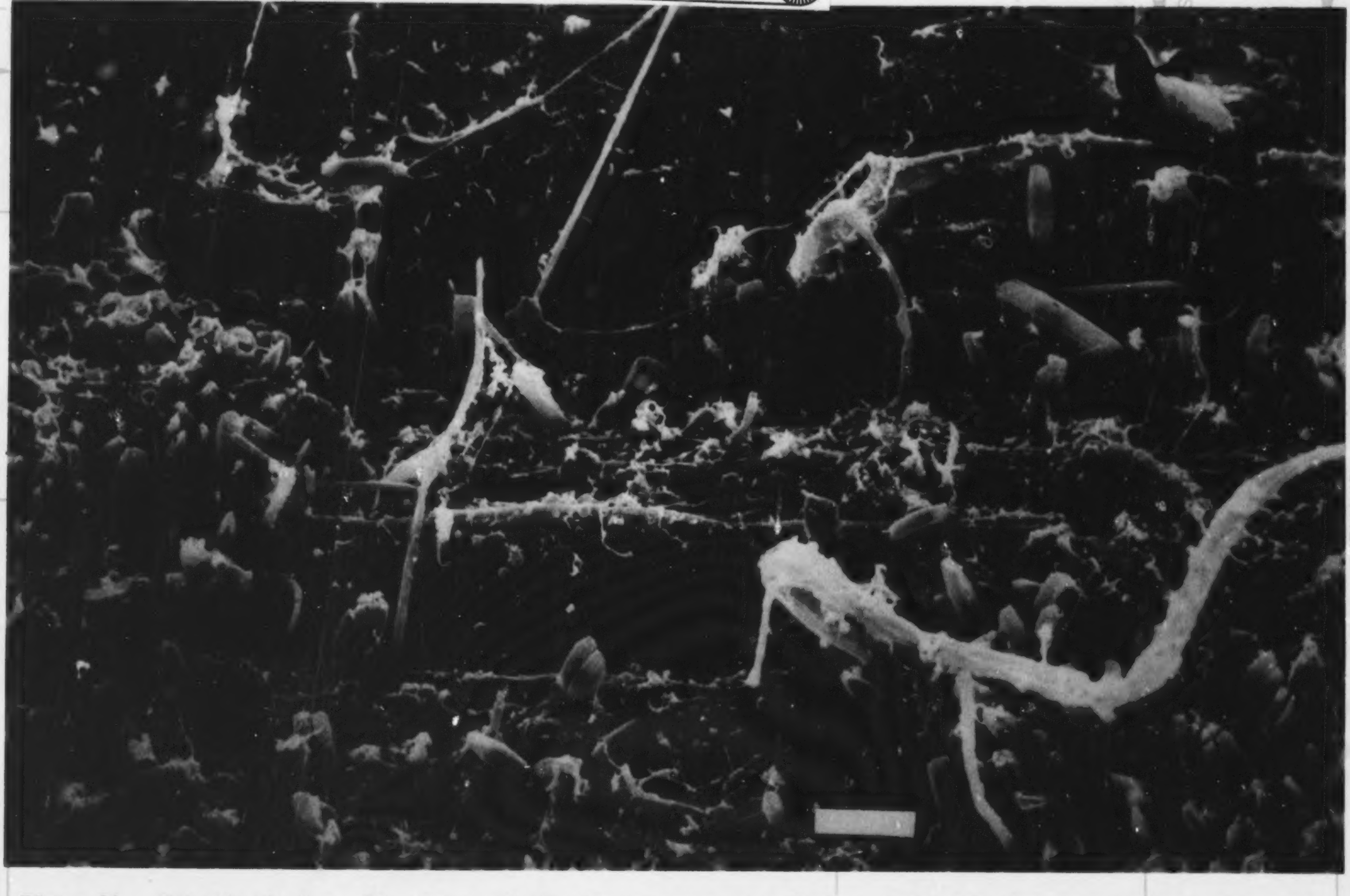

Plate 24. Detail of plate 23. Most of the diatoms are attached on end with the majority concentrated in cracks in the artificial blade (1500X; size bar = 10 µm).

habitats may be essential in maintaining viability of the seagrasses, especially under nutrient-rich conditions.

We utilized artificial substrates to quantify the impact of *Bittium varium* grazing on periphyton. However, the use of inert substrates in assessing the quantity and quality of periphyton found on natural macrophytes is a subject of much debate. The importance of nutrient transfer and other metabolic interactions between macrophytes and their epiphytic colonizers (see Moss, 1981; Eminson and Moss, 1980 for review) has been recognized for freshwater systems. External environmental factors determine periphyton community composition in marine systems (see Harlin, 1980 for review). However, a recent study (Eminson and Moss, 1980) demonstrated that greater macrophyte host specificity by microalgae occurred in oligotrophic lakes than in lakes with moderate to high nutrient loading. Under eutrophic conditions host specificity was progressively less apparent and periphyton communities became similar between all submerged vascular plant species, despite differences in macrophyte surface texture and metabolic activity. It is possible that the distinct differences we observed in periphyton species composition between polypropylene ribbon and live eelgrass was caused by the actively metabolizing, cobblestone textured leaves of the living plants.

We have demonstrated that grazing resulted in a significant reduction of periphyton biomass on polypropylene ribbon. Since an analysis of phaeopigments (and not chlorophyll *a*) showed differences paralleling the gravimetric analyses, implications are that the periphytic crust utilized by *Bittium varium* in these experiments was predominantly senescent. Scanning electron micrographs of the artificial blades revealed that the epiphytic complement differed considerably from that found on live *Zostera marina*. Grazing impacts of *B. varium* on periphyton of both substrates, however, are comparable. SEM photographic evidence of short term feeding activities supports the fact that *B. varium* grazing reduces or removes the periphytic community on natural blades.

Bittium varium grazing sometimes affects the structure of the diatom population. This is accomplished by the mechanically selective removal of all loosely adhering species such as *Amphora* sp. and *Nitzschia* sp. which inhabit the upper portion of the periphyton crust. *Cocconeis scutellum* is able to firmly attach to the *Zostera marina* epithelium by a mucilagenous secretion thereby avoiding extensive grazing by *B. varium*. Thus, the grazing activity of *B. varium* may facilitate community dominance by *C. scutellum*, a species which has been previously identified as the most ecologically and numerically important diatom on *Z. marina* (Sieburth and Thomas, 1973; Jacobs and Noten, 1980).

The shading imposed by epiphytes on their seagrass host can be severe enough to either restrict their vertical distribution (Caine, 1980) or cause the complete disappearance of the macrophytes (Sand-Jensen, 1977; Moss, 1981; Eminson and Moss, 1980). The removal of most periphyton from artificial blades by grazing and evidence of similar removal from live *Zostera marina* suggests that *Bittium varium* plays an important role in mediating the proliferation of epiphytic diatoms on these substrates. The disruption of the periphyton grazer component (as is the case with the elimination of *B. varium* from seagrass habitats along the western shore of the Chesapeake Bay) could seriously alter the steady state of periphyton abundance to the detriment of the host plant. The preliminary results of our work indicate that a more detailed and quantitative study of the macrophyte-periphyton-micrograzer relationship is necessary to substantiate this hypothesis as a partial explanation for demise of *Z. marina* in certain areas of the Bay.

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CHAPTER 6

WATERFOWL UTILIZATION OF A SUBMERGED VEGETATION (*ZOSTERA MARINA* AND *RUPPIA MARITIMA*) BED IN THE LOWER CHESAPEAKE BAY[1]

by

Elizabeth W. Wilkins

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[1] A thesis presented to the Faculty of the School of Marine Science, The College of William and Mary, Williamsburg, Virginia

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Waterfowl specimens were collected by Vernon Leitch, Buck Wright and Curtis Jones of Northampton County, and Louise and Bart Theberge of the Virginia Institute of Marine Science. Rich DiGiulio, of Virginia Polytechnic Institute, provided a number of specimens, as well as valuable discussion and good company, while collecting in the area for his own research.

Martha and Vernon Leitch, Vaucluse Pt. residents, deserve special thanks for their warmth and hospitality during the bitter cold months.

ABSTRACT

A study of waterfowl use of a bed of submerged aquatic vegetation was conducted over two winters in the Lower Chesapeake Bay (Virginia). In the season of 1978-1979, Canada geese (Branta canadensis) were the dominant waterfowl in the study area. Goose foraging activity was correlated with tide stage, and was greatest at low tide. Consumption by grazing waterfowl was calculated from bird densities, and was approximately 25% of the standing crop of vegetation in the shallow portion of the habitat. In 1979-1980 diving ducks, primarily buffleheads (Bucephala albeola), were dominant. Abundance of waterfowl was influenced by wind parameters, but tide, temperature and time of day hlad little or no influence on bird numbers. Within-habitat variation in abundance was examined, and highest densities were associated with the deeper Zostera marina zone.

Gizzard samples and $\delta^{13}C$ analysis revealed that buffleheads fed primarily on small gastropods and nereid worms characteristic of the grassbed epifauna. Consumption of important invertebrate prey items, calculated from exclosure experiments and waterfowl densities, amounted to nearly 50% of the fall standing crop of these species in Zostera marina.

INTRODUCTION

Submerged aquatic vegetation (SAV) is widely recognized as a valuable food resource for wintering waterfowl populations (Bent 1923, Cottam 1939, Stewart 1962, Bellrose 1976, Munro and Perry 1981). The demise of *Zostera marina* during the 1930's was thought to cause the precipitous decline of the Atlantic brant (*Branta bernicla hrota*) (Cottam 1934, Addy and Aylward 1944, Cottam and Munro 1954), although coincidence of poor reproductive success may also have been important in reducing populations (Palmer 1976). Numbers of waterfowl utilizing the traditionally important Susquehanna Flats as a winter feeding ground in the Chesapeake Bay plummeted during the height of the eurasian water milfoil epidemic in the 1960s, but returned to former levels after native aquatics became re-established (Bayley et al. 1978).

Recent surveys indicate that submerged vegetation has declined in most areas of the Chesapeake Bay in the last 15 years (Bayley et al. 1978, Anderson and Macomber 1980, Orth and Moore 1981). The response by several waterfowl species has been to alter feeding habits or distribution patterns rather than sustain population losses (Munro and Perry 1981). Canvasbacks (*Aythya valisineria*) once fed primarily on wild celery (*Vallisneria americana*), but since the early 1970's have fed mostly on bivalves (primarily *Macoma balthica*; Perry and Uhler 1976). Canada geese (*Branta canadensis*) and to a lesser extent whistling swans (*Cygnus columbianus columbianus*), now rely on agricultural grain as a major dietary component on the wintering grounds (Bellrose 1976). Other species such as redheads (*Aythya americana*), wigeon (*Anas americana*) and pintails (*Anas acuta*), which indicate a continued preference for SAV, have declined in the Bay in recent years, and it is likely that their winter distribution now coincides with areas of greater SAV abundance (Munro and Perry 1981).

Past or current preference for submerged vegetation in the diet is well documented for the above species (Martin and Uhler 1951, Stewart 1962, Munro and Perry 1981). With the exception of canvasbacks and redheads, all are non-divers, or dabblers, which feed in shallow water by tipping up rather than diving to obtain food. Many diving species also feed in SAV habitats on benthic invertebrates. Animal communities associated with grassbeds differ markedly from those in unvegetated areas, both in structural and functional aspects. Submerged aquatic vegetation supports a dense and diverse epifaunal assemblage not found on bare substrates (Marsh 1970), and organisms living on or within sediments are also more abundant due to greater sediment stability and microhabitat complexity (Thayer et al. 1975, Orth 1977). Grassbeds should therefore attract waterfowl which feed on invertebrates as well as those which rely on vegetation, although there is scant evidence to this effect. Nilsson (1969) reported that in shallow water in the Oresund, Sweden, two diving duck species studied fed preferentially over Zostera marina and one fed over patchy Ruppia sp. and Z. marina, whereas an intervening belt of vegetation-free sand contained no fauna of trophic importance for these species.

In spite of the food resources available to waterfowl in SAV habitats, Munro and Perry (1981) found few significant relationships between the distribution and abundance of submerged vegetation and waterfowl populations in the upper Chesapeake Bay. Several species, such as whistling swans, black ducks (Anas rubripes), mallards (Anas platyrhynchos) and buffleheads (Bucephala albeola), showed positive associations with SAV in certain areas, but results were not consistent over all survey zones. In the Lower Bay, the current relationship between waterfowl and SAV is largely unknown. The purpose of this research was to provide detailed information regarding waterfowl use of a particular bed of submerged vegetation in the Lower Bay. Specific objectives were to examine short term patterns of utilization, and to identify and estimate consumption of important waterfowl foods within the study area.

Waterfowl foraging studies have traditionally emphasized gizzard analysis, but more recent research has sought to quantify consumption in addition to describing food habits. A common approach employs average population estimates, theoretical daily ration based on body weight, and knowledge of trophically important foods to arrive at values for annual consumption. These values may then be compared with either standing crop or production of food items to determine grazing or predation pressure. In the saline Lake Grevelingen, The Netherlands, Wolff et al. (1975) and Neinhuis and van Ierland (1978) reported that waterfowl consumed less than 1% of the annual production of Zostera marina, whereas Jacobs et al. (1981) calculated that consumption by waterfowl amounted to 50% of the standing crop of Zostera noltii near Terschelling, The Netherlands. Intermediate values for grazing pressure have been obtained by other investigators using similar methods (Sincock 1962, Steiglitz 1966, Cornelius 1977). Another technique compares biomass samples taken before arrival and after the departure of seasonally-resident birds (Ranwell and Downing 1959, Burton 1961). Values obtained in this way tend to overestimate consumption during the non-growing season, as seasonal declines related to physical factors are also included in these estimates (Charman 1977).

Exclosure experiments have provided additional estimates of consumption, using differences in biomass between grazed and ungrazed (caged) plots to quantify waterfowl feeding. Verhoeven (1978) used exclosures to estimate the impact of foraging by European coots (Fulica atra) and found a marked reduction in the biomass of Ruppia cirrhosa outside exclosures. Jupp and Spence (1977) protected plots of Potamogeton spp. in Loch Leven, Scotland, and reported a similar decline in plant biomass due to waterfowl grazing. Charman (1977) did not estimate grazing pressure, but attributed early seasonal depletion of Zostera to the foraging activities of brent geese based on the results of his previous exclosure experiments.

Similar information for non-grazing waterfowl is almost entirely lacking. Nilsson (1969) calculated that diving ducks consumed less than 10% of the standing crop of invertebrates in a Zostera and Ruppia bed. Sincock (1962) estimated consumption by a number of non-grazing waterfowl but did not relate these values to standing crop. The diversity and patchy distribution of potential food organisms, and the difficulties associated with gizzard analysis may account for the lack of quantitative data.

A technique recently employed to characterize trophic relationships in seagrass communities involves analysis of stable carbon isotope ratios in tissues of herbivores or higher-level consumers. Based on differential uptake of ^{13}C by plants, ^{13}C:^{12}C ratios (expressed in $\delta^{13}C$ units) have been used to identify primary sources and fluxes of organic carbon in grassbeds and other habitats. Comparisons of animal $\delta^{13}C$ values with known or estimated dietary values indicate that isotope ratios are conserved through the food chain (Haines 1976, Fry et al. 1978, Haines and Montague 1979), with only slight variation due to effects of metabolic fractionation (De Niro and Epstein 1978). Seagrasses exhibit $\delta^{13}C$ values of -3 to -13°/oo which are readily distinguished from those of phytoplankton (-18 to -24.5 °/oo), with benthic diatoms having intermediate values (Fry and Parker 1979). Resolution of dietary components is thus limited to fairly broad taxonomic or functional groups, but the technique is much less tedious than examination of gut contents.

Application of $\delta^{13}C$ analysis to waterfowl trophic studies has thus far been limited, but suggests a similar strong relationship between isotope ratios of bird tissue and dietary values. Patrick Parker and James Winters (pers. comm.) have used $\delta^{13}C$ values from liver and other tissues to study redheads foraging in shoalgrass (Halodule wrightii). Bird $\delta^{13}C$ values exhibited a positive seasonal shift of about 8 °/oo soon after arrival of birds from the breeding grounds, indicating rapid carbon turnover in bird tissue associated with the new winter diet. McConnaughey and McRoy (1979) reported a similar seasonal shift in values for waterfowl species in the Izembek Lagoon, Alaska. Although turnover may be very rapid, dietary information is time-integrated in the short term, whereas gizzard samples represent single foraging episodes.

Details of diet and reliable consumption estimates are needed to assess the functional role of waterfowl in SAV habitats and to evaluate the importance of this resource for wintering waterfowl. In this study, several of the above methods were combined, as it was felt that an integrative approach would provide more information than the use of a single technique, and would allow for comparison of results obtained by different methods.

METHODS

The Study Area

Vaucluse Shores is located on the Delmarva Peninsula in the lower Chesapeake Bay, just north of Hungar's Creek in Northampton County, Virginia (37°25'N latitude, 75°39'W. longitude) (Figure 1). The site consists of approximately 150 hectares vegetated subtidally by *Ruppia maritima* and *Zostera marina* (hereafter *Ruppia* and *Zostera*) which dominate beds of submerged vegetation in meso- and polyhaline regions of the Bay. These species are distributed according to depth, with *Ruppia* dominant in shallow water [less than 0.5 m at mean low water (MLW)], *Zostera* dominant in deeper water (greater than 1.0 m) and a mixed vegetation zone present at intermediate depths. Areal extent of the grassbed is delimited bayward by a series of parallel offshore sandbars oriented obliquely to the shoreline. Six transects (A-F) were established in the study area in 1978 for use in mapping vegetation at the site (Orth et al. 1979) and these provided convenient boundaries for waterfowl censuses.

Biomass data for *Zostera* at Vaucluse Shores indicate a seasonal maximum coinciding with seed production in June and July, averaging 85 g m^{-2} in 1978 (Orth et al. 1979). A second smaller peak in biomass takes place in the fall, followed by winter values of less than 50 g m^{-2}. *Ruppia* has a slightly different growth cycle, with one major biomass peak occurring in August and September. Both species may exhibit different patterns of growth at mixed vegetation sites (P. A. Penhale, pers. comm.).

Salinity at the site varies from 14 ^{o}/oo to 24 ^{o}/oo and water temperatures range from -2C to 28C. In winter months, extreme low temperatures may cause ice formation in the shallow areas.

The same site was the focus of a broad scale interdisciplinary study (EPA-CBP contract #R80-59-74) designed to describe the principal components of seagrass communities in the lower Chesapeake Bay, and to elaborate important aspects of the functional ecology of these systems. This integrated program included the following investigation of waterfowl use of the habitat.

Waterfowl Abundance Estimates

1978-79: A preliminary census effort was undertaken in 1978-79 consisting of 13 census days between 6 December and 22 March, with a variable number of censuses per day. Waterfowl observed between previously established transects A through F were identified and counted with the aid of a spotting telescope and located by transect interval. The duration of each census was 15 minutes, and all birds present during that time were counted. Feeding activity of Canada geese was noted, and the relationship between percent feeding and tide level was tested using the Spearman rank-correlation coefficient r_s, computed as

$$r_s = 1 - \frac{6^{\,n} (R_1 - R_2)^2}{n(n^2 - 1)}$$

where R is the variable rank, and n is the sample size (Sokal and Rohlf 1981). Census times were used to obtain approximate tide level data from NOAA tide prediction tables.

1979-80: All observations were made between transects B and C (Figure 1) in 1979-80, allowing a more intense effort in a smaller area (approximately 26.5 ha) which had been consistently utilized by waterfowl the previous year. Waterfowl were censused at intervals averaging 11 days from 8 November to 3 April and on each census date birds were counted at approximately 2-hourly intervals during daylight.

At the outset of the study, four zones were marked in the census area from shore to the offshore sandbar which encloses the grass bed: bare sand, patchy Ruppia maritima, mixed Ruppia and Zostera, and pure Zostera marina. Although the zones are not highly discrete, fluorescent stakes were placed at transitions along transects B and C such that major vegetation type was indicated between pairs of stakes. The position of each bird was recorded in reference to these stakes. In order to express waterfowl numbers in terms of vegetation type, areal extent of each zone was estimated from the results of vegetational transect analysis reported by Wetzel et al. (1979) and from personal observation of transition zones. Density of waterfowl within these zones was then calculated, and differential utilization was tested between each pair by the Wilcoxon nonparametric two-sample rank test. The Wilcoxon statistic is calculated for samples of equal size as follows:

$$C = n^2 + \frac{n(n + 1)}{2} - \sum^{n} R$$

where n is sample size and R is the variable rank. This statistic is then compared with $(n^2 - C)$ and the greater of the two quantities is the test statistic U_s (Sokal and Rohlf 1981). The bare sand zone was excluded from analyses, as waterfowl rarely utilized that area.

A tide gauge consisting of a stake graduated in 5 cm increments was placed in subtidal shallow water and water level was recorded at the time of each census. The stake was destroyed by ice floes and replaced twice, but after 1 February tide data were obtained from NOAA tables as in 1978-79. Time and air temperature were also recorded, and wind speed and direction were obtained from the National Weather Service station in Norfolk, Virginia. The above parameters were related to waterfowl abundance using nonparametric correlation statistics as described above. In the case of tide, separate correlations were run for each vegetation zone in order to minimize the effect of the onshore-offshore depth gradient. One census date, 23 March, was eliminated from the above correlations because of the

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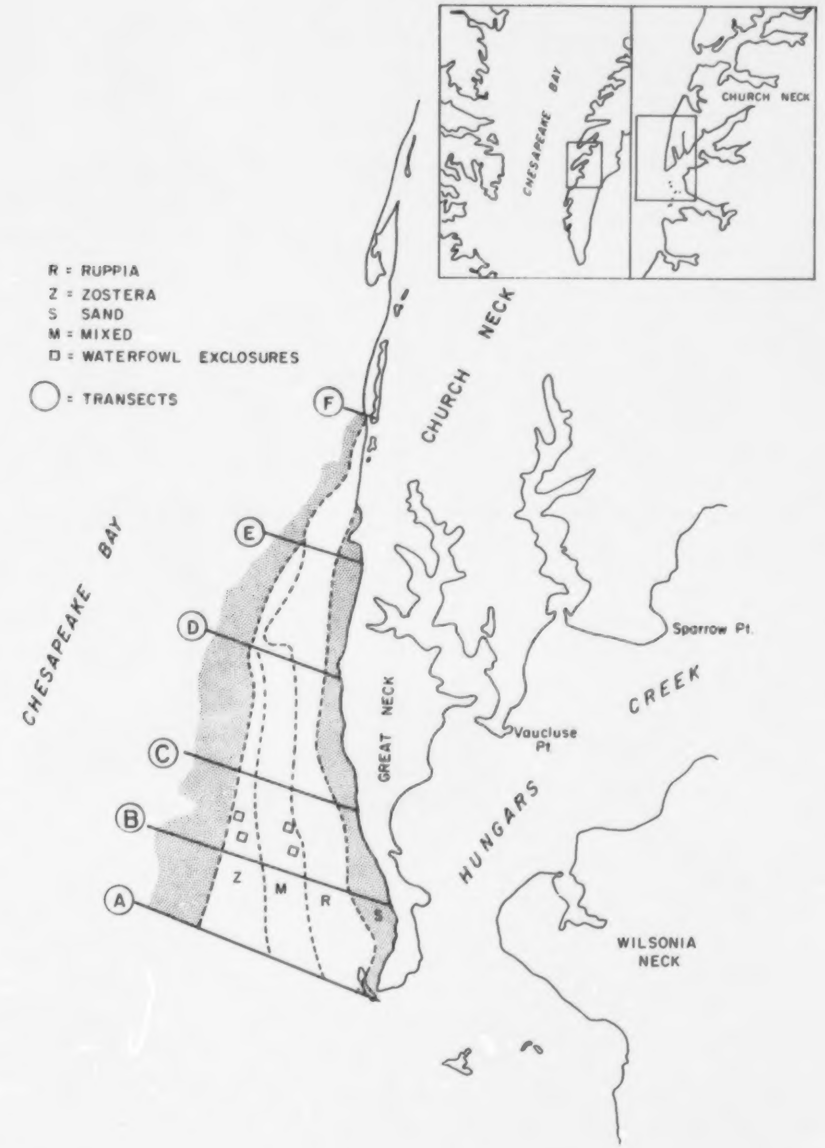
R = RUPPIA
Z = ZOSTERA
S = SAND
M = MIXED
□ = WATERFOWL EXCLOSURES
○ = TRANSECTS
CHESAPEAKE BAY
CHURCH NECK
A
B
C
D
E
F
Z
M
R
S
GREAT NECK
Sparrow Pt.
Vaucluse Pt
HUNGARS CREEK
WILSONIA NECK

Fig. 1. The Vaucluse Shores study area, showing previously established transects A-F, and the location of waterfowl exclosures within transect interval B-C.

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presence of a single large flock of redheads which would have obscured major trends.

Food Habits

Waterfowl gizzards and livers were obtained from birds collected by local hunters and scientific personnel in the study area and in the mouth of Hungar's Creek between October 1979 and March 1980. Because buffleheads were predominant in the second year of study, the diet of this species was the focus of food habits studies. Bufflehead gizzards were analyzed for food items, and livers of all species were analyzed for stable carbon isotope ratios ($\delta^{13}C$). Gizzards were kept frozen before laboratory processing, and contents were then sieved into two fractions for ease of examination. The coarse and fine fractions were retained on 0.5 mm and 62μ sieves, respectively. Material which passed through the 62μ sieve was negligible and therefore was discarded. Both fractions were preserved in 10% formalin. Contents of intact esophagi were examined, but were sieved on 62μ mesh only.

Identifiable species were enumerated under a dissecting microscope and noted as present or absent in the case of fragmented remains. Total contents of individual gizzards were not weighed, as it was felt that differential digestion would bias these quantities to a great extent. Instead, a representative sample of entire specimens of each prey species was obtained and dried to constant weight. Ash-free dry weights were estimated using conversion factors in Cummins and Wuycheck (1971) and values provided by J. Lunz and D. Weston (pers. comm.) for two mollusc species, as follows:

Peracarida	0.82 x Dry weight
Annelida	0.82
Decapoda	0.74
Mollusca	0.10 (For *Bittium varium* and *Crepidula convexa*)

These weights were multiplied by abundance per gizzard in order to calculate percent composition by dry weight and ash-free dry weight. The aggregate percent method was used to calculate mean composition, where the proportion of a species in each gizzard is averaged over all gizzards (Swanson et al. 1974). By this method, each gizzard has equal importance despite differences in volume of contents. Dietary importance was determined using the 'index of relative importance' (IRI) (Pinkas et al. 1971):

$$IRI = (\%\ N + \%\ W) \times \%\ F$$

where N is numerical abundance, W is weight, (substituted here for volume) and F is frequency of occurrence.

Bufflehead dietary electivity was calculated within mollusc prey species only, as the numerical importance of softer-bodied forms may not be as accurately reflected in gizzard samples. The Jacobs index

(L) was used to measure electivity because the degree of departure from zero (non-selectivity) can be statistically tested (Gabriel 1978). L is calculated as follows:

$$L = \ln (O) \text{ where } O = \frac{p_1 q_2}{p_2 q_1}$$

and p_1 = proportion of diet comprised by a given prey taxon
q_1 = proportion of diet comprised by all other prey taxa
p_2 = proportion of food complex in environment comprised by given taxon
q_2 = proportion of food complex in environment comprised by all other taxa

Estimates of environmental abundance of prey items were obtained from cores collected in January, and only gizzard samples which were collected within two weeks of benthic sampling were used to obtain dietary values.

Stable Carbon Isotope Analysis

Waterfowl livers were rinsed in distilled water, dried at 65°C for 96 hr and ground in a Wiley Mill to a fine powder. These samples were analyzed by Dr. Evelyn Haines at the University of Georgia Marine Science Institute and Drs. Patrick Parker and James Winters of Coastal Science Laboratories, Inc., at Port Aransas, Texas. Details of further sample preparation and analyses by these labs are described in Haines (1976) and Parker et al. (1972), respectively. In general samples are first combusted to convert organic carbon into CO_2, which is then isolated from other evolved gases. Isotopic analysis of CO_2 is carried out on a mass spectrometer, and isotope ratios are reported relative to a carbonate standard, in $\delta^{13}C$ units (parts per mil):

$$\delta^{13}C = \left(\frac{{}^{13}C/{}^{12}C \text{ sample}}{{}^{13}C/{}^{12}C \text{ standard}} - 1 \right) \times 10^3$$

Tissues of important waterfowl foods (invertebrates from the study area) were prepared and analyzed in the same manner, except that in many cases specimens were pooled to obtain sufficient tissue (≈60 mg). For comparison with observed bufflehead $\delta^{13}C$ values, an expected value was calculated by multiplying the mean percent contribution of each prey species to the diet (ash-free dry weight) by its $\delta^{13}C$ value, and summing these values over all gizzards (Fry et al. 1978).

Waterfowl Exclosure Experiments

To investigate the impact of grazing waterfowl (primarily Canada geese and redheads) on vegetation density at the study site, two areas between transects B and C were chosen to locate exclosures: a shallow mixed _Ruppia_ and _Zostera_ zone and a deeper pure _Zostera_ zone (Figure

1). Between 14 and 18 October 1979, two caged plots were established in each of these zones at depths of approximately 0.5 m and 1.2 m at MLW, respectively. Cage pairs included one cage (cage I) to be sampled at two intervals during waterfowl residence and another (cage II) to be sampled only if cage I was damaged.

Exclosures measured 2m x 2m x 0.5m and were constructed with 2.5 cm mesh vinyl-coated wire sides and crab pot wire tops (2.5 cm hexagonal mesh), hinged on two sides to open from the center during sampling. A frame consisting of a length of shaped concrete reinforcing rod supported the top and penetrated the sediment to 50 cm. In addition, a 1 m length of reinforcing rod was attached to each corner and buried to 50 cm.

Benthic samples were taken with a 0.031 m^2 plexiglass corer to a depth of approximately 15 cm during three sampling periods: 18 October 1979, 16-19 January 1980, and 19 March 1980. On 18 October, six replicate cores were taken in the vicinity of cages located in the Zostera and mixed vegetation zones. Sample size was chosen based on previous estimates of variability in plant biomass in the study area (Orth et al. 1979). These samples were processed for vegetation only, which was separated into above and below ground fractions, then dried in an oven at 55°C for 48 hours and weighed.

During the second sampling period methodolgy was modified based on the near-absence of Canada geese from the grassbed (see results). As the dominant species was the bufflehead, which feeds primarily on invertebrates (Stewart 1962), samples were processed for animal abundance as well as quantity of vegetation. Sample size was increased to ten cores each from caged and uncaged sites to account for greater patchiness of the invertebrate species.

Cores from uncaged areas were taken in a pattern radiating from the center of the cage using random compass headings and distances between 6 m and 12 m from the cage. Within exclosures, cores were taken randomly from a 2m x 2m grid. Care was taken to position and remove the corer with the least possible disturbance to adjacent bottom. Samples were placed in muslin bags, refrigerated and washed the following day on a 0.5 mm sieve. Cores collected in January were frozen after sieving, but this resulted in damage to soft-bodied invertebrates and thus samples collected in March were stored in 10% formalin.

In the lab, samples were rinsed and elutriated repeatedly to separate vegetation from the animal and sediment component, which was then sieved into two fractions. The coarse fraction (>2 mm) was sorted and identified in its entirety, and the fine fraction (<2 mm >0.5 mm) was distributed evenly on the sieve by flotation and then split into quarters. Two quarters were chosen randomly for sorting and the counts obtained were then doubled. Split counts were compared to total counts for two samples. Total number of individuals was 3.0% in error for one comparison and 3.1% for the other. Error by species varied, with the rarest species most affected by the technique. All organisms were identified to lowest taxa, with some exceptions. In the January samples polychaetes, oligochaetes, and nemertea were eliminated from analysis because damage from freezing rendered numbers unreliable. Only two dominant epifaunal polychaetes, *Nereis succinea* and *Polydora ligni*, were identified to species in the March samples.

Sediment cores were taken to determine effects of exclosures on sedimentation processes. Three cores were taken from each treatment in January and five were taken from each treatment in March. Percent sand and silt-clay were determined by sieving and pipette analysis outlined by Folk (1961).

Differences between treatment means were tested using the Wilcoxon statistic, with the exception of sediment data, which were arcsin transformed (Sokal and Rohlf 1981) and compared between treatments using a standard t-test.

Estimates of Consumption from Waterfowl Density

Mean waterfowl abundances, theoretical daily intake, and days in residence were used to estimate total consumption of biomass by birds utilizing the study area. Methods for determining daily intake are from Wolff et al. (1975) where standard metabolism M is multiplied by 5 to obtain consumption in kcal/day. M is determined by the formula:

$$\text{Log } M = \text{Log } 78.3 + 0.723 \text{ log} W$$

where W is body weight in kg. Kcal were converted to grams ash-free dry weight (AFDW) by multiplying by a factor of 0.2. These values were then used in the following formula for consumption:

$$C = I \cdot A \cdot R$$

where I = daily intake in grams AFDW
A = mean abundance
R = residence (estimated as 150 days)

Consumption was calculated over the total habitat as well as more restricted areas, based on patterns of utilization within the habitat. Estimates were partitioned according to predominant feeding type (animal vs vegetation) according to Stewart (1962) and Munro and Perry (1981).

RESULTS

Waterfowl Abundance

1978-79: The Canada goose was the most important waterfowl species in the study area in 1978-79, and averaged 526 individuals per 100 hectares (Table 1). The overwhelming dominance demonstrated by

TABLE 1. MEAN ABUNDANCES OF WATERFOWL SPECIES AT VAUCLUSE SHORES 1978-1979.

		Birds Per 100 Hectares													
		1978		1979											Overall Mean Abundance (Weighted)
		12/6	12/24	1/7	1/8	1/9	1/10	1/27	2/3	2/4	2/17	2/18	3/7	3/22	
	# Censuses	1	1	5	1	4	5	3	4	4	8	4	4	10	
Canada goose (Branta canadensis)	$\overline{x}$	964	4052	1965	0	34	531	1623	168	147	194	643	6	52	526.5
	±S.E.	--	--	±198.1	--	±33.8	±413.3	±812.3	±141.00	±99.5	±79.6	±80.2	±6.2	±17.3	
Bufflehead (Bucephala albeola)	$\overline{x}$	17	3	19	35	35	39	85	59	51	35	102	41	46	46.1
	S.E.	--	--	±26.8	--	±4.2	±9.5	±20.2	±19.9	±29.0	±12.2	±64.1	±10.2	±12.3	
Redhead (Aythya americana)	$\overline{x}$	0	0	48	61	30	0	0	0	0	91	302	0	0	44.2
	S.E.	--	--	±30.7	--	±67.5	--	--	--	--	±113.9	±191.6	--	--	
Brant (Branta bernicla)	$\overline{x}$	0	0	0	0	0	0	0	1	0	0	404	0	0	29.9
	S.E.	--	--	--	--	--	--	--	0.8	--	--	±348.8	--	--	
Red-breasted merganser (Mergus serrator)	$\overline{x}$	0	0	43	135	0	0	0	0	33	0	0	32	28	18.9
	S.E.	--	--	±27.6	--	--	--	--	--	±27.2	--	--	±11.3	±12.0	
American wigeon (Anas americana)	$\overline{x}$	0	0	64	23	5	4	0	0	8	0.2	38	13	3	12.0
	S.E.	--	--	±17.9	--	±4.8	±2.5	--	--	±7.8	±0.2	±27.6	±12.4	±1.7	
Whistling swan (Cygnus columbianus)	$\overline{x}$	15	15	7	23	0	7	0	0	0	12	3	1	0	4.4
	S.E.	--	--	±4.1	--	--	±5.1	--	--	--	±6.9	±1.7	±1.2	--	
Pintail (Anas acuta)	$\overline{x}$	0	0	13	0	6	9	0	0	0	1	2	0	0	2.7
	S.E.	--	--	±9.2	--	±6.5	±9.0	--	--	--	±0.8	±1.8	--	--	
Black duck (Anas rubripes)	$\overline{x}$	0	0	1	0	0	0	0	1	8	1	14	1	2	2.2
	S.E.	--	--	±11.9	--	--	--	--	±1.8	±3.9	0.8	±12.8	±0.3	±0.9	
Common goldeneye (Bucephaea clangula)	$\overline{x}$	0	0	2	0	0	1	1	0	1	0	0	2	0.4	2.2
	S.E.	--	--	±1.8	--	--	±1.3	±1.1	--	±0.7	--	--	±1.8	±0.1	
Scaup sp. (Aythya spp.)	$\overline{x}$	0	0	0	0	0.4	0	0	0	0	0	12	0	0	0.9
	S.E.	--	--	--	--	±0.4	--	--	--	--	--	±12.5	--	--	
Surf scoter (Melanitta perspicillata)	$\overline{x}$	0	0	0	0	--	2	0	3	0	0	0	0	0	0.4
	S.E.	--	--	--	--	--	±1.8	--	±1.5	--	--	--	--	--	
Mallard (Anas platyrhynchos)	$\overline{x}$	0	0	2	0	0	0	0	0	0	1	0	0	0	0.3
	S.E.	--	--	±1.3	--	--	--	--	--	--	±1.2	--	--	--	

the species is obvious when plots of total waterfowl and Canada goose abundance are compared (Figure 2). Second in importance was the bufflehead, which averaged 46 birds per 100 ha and was the only species present on every census date. Large flocks of redheads utilized the study area, but occurred on only 5 of the 13 census days. It is uncertain whether this species was adequately censused, as foraging may have been primarily nocturnal. Redheads were most often observed at dawn and dusk, and did not generally remain in the area throughout the day.

Brant occurred on only two census dates, but one flock of approximately 1300 birds inflated the relative importance of the species. Whistling swans and wigeon were present regularly (in more than 60% of censuses) but in low numbers. Red-breasted mergansers (Mergus serrator) occurred less frequently but in flocks with an average density of 19 birds per 100 ha. Although non-divers (primarily Canada geese) were more abundant than diving ducks, both groups were represented by nearly equal numbers of species throughout the season.

Abundances of most species fluctuated without respect to seasonality in 1978-79. However, Canada geese were most abundant in the first few censuses, and this trend would probably have been more pronounced had the earliest part of the season (November to early December) been included.

Utilization of the study area by foraging Canada geese was influenced by tide level (Figure 3). At the lowest water levels (2 hr. before and after low tide) the majority of geese present were feeding, whereas geese almost never attempted to feed at higher tide levels, and instead remained on the offshore sandbar. A negative rank correlation between percent feeding and departure from low tide in hours was significant at $p < 0.001$.

1979-80: Patterns of waterfowl abundance changed dramatically in the second year of observations. Fewer species utilized the area consistently (four per day average) and the proportion of non-diving to diving species decreased to less than 0.2 per day (Figure 4). Although large numbers of Canada geese were noted in the vicinity of Hungar's Creek, no large flocks were censused within the study area (Table 2). During a number of censuses, rafts of several hundred geese were observed directly offshore at a distance of approximately 500 m beyond the sandbar (numbers in parentheses in Table 2), but they did not come into the grassbed.

The bufflehead was the dominant species in 1979-80, and total waterfowl numbers closely tracked the abundance of this diving duck (Figure 5). Again, they occurred on every census date, and mean density of this species (96 birds per 100 ha) was approximately twice as great as in 1978-79. Redheads were also important though infrequent the second year, primarily due to a flock of approximately 500 birds which fed in shallow Ruppia on 6 March. In contrast to the

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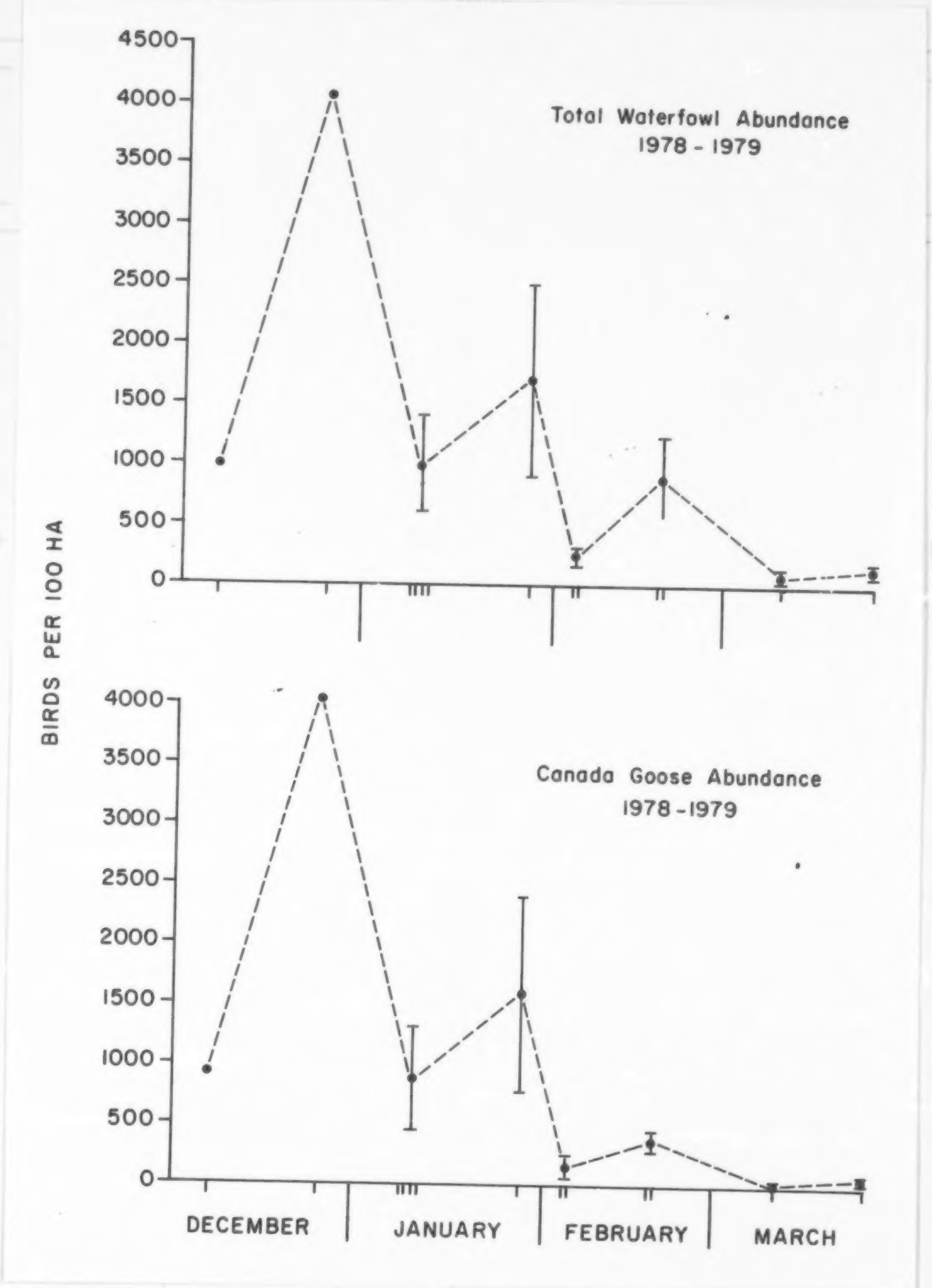

Fig. 2. Abundances of total waterfowl and Canada geese at Vaucluse Shores, 1978-1979. Points represent means and bars are standard errors of the mean.

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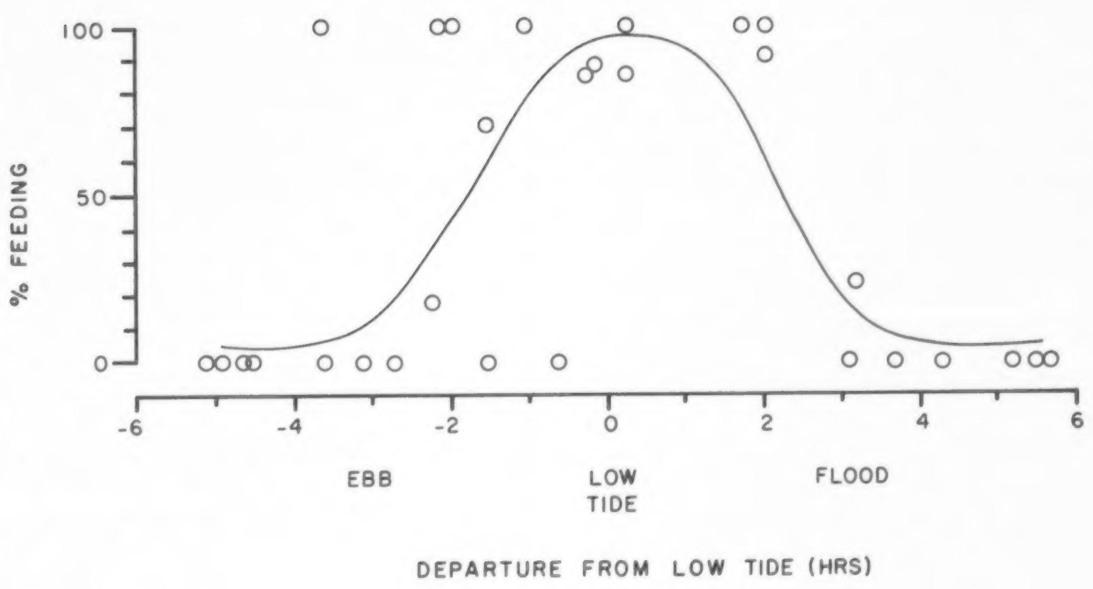

Fig. 3. Relationship between tide stage and foraging activity in Canada geese at Vaucluse Shores, 1978-1979. Curve fit by eye.

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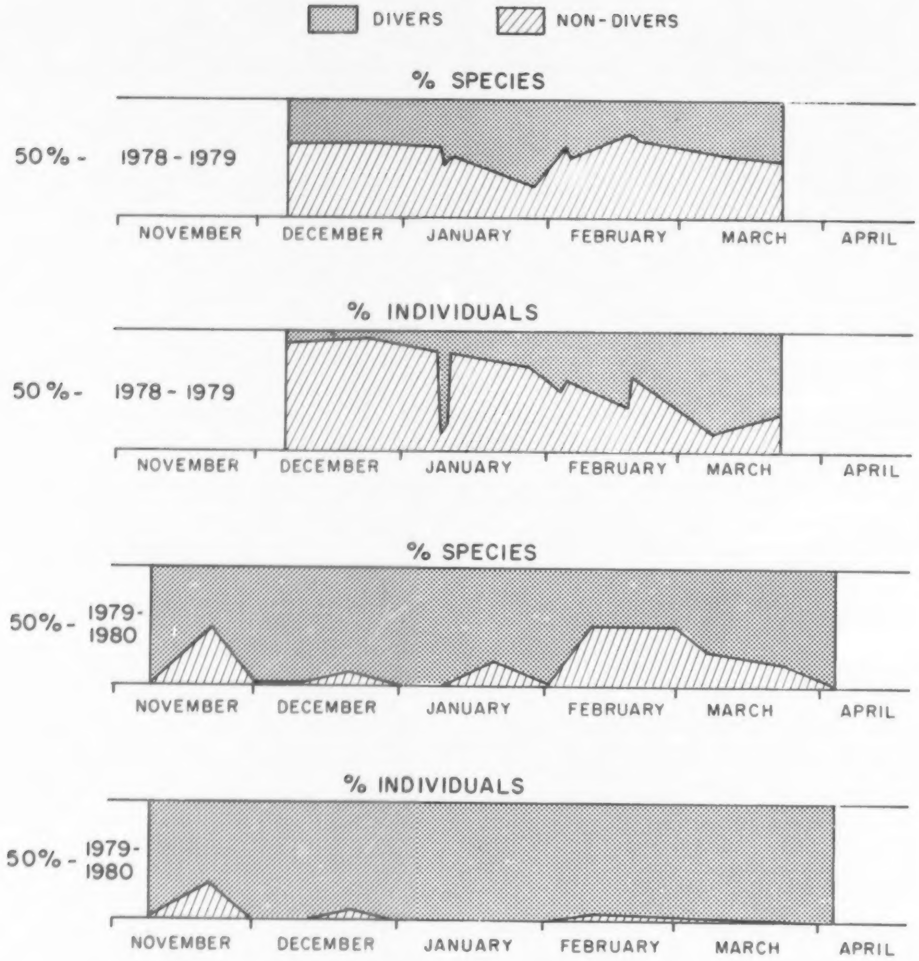

Fig. 4. Numbers of diving vs. non-diving waterfowl, as a percentage of total waterfowl during 1978-1979, compared to 1979-1980.

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TABLE 2. MEAN ABUNDANCES OF WATERFOWL SPECIES AT VAUCLUSE SHORES, AREA B-C, 1979-1980.

		Birds Per 100 Hectares														
		1979						1980								Overall Mean Abundance (Weighted)
		11/8	11/20	11/30	12/10	12/21	12/28	1/9	1/20	2/1	2/10	2/27	3/6	3/23	4/3	
	# Censuses	6	6	6	6	6	6	5	6	6	5	6	6	7	7	
Bufflehead (Bucephala albeola)	$\bar{x}$	51	46	126	153	56	85	113	149	69	115	114	46	145	78	96.1
	±S.E.	±16.9	±19.8	±18.8	±23.0	±25.6	±24.2	51.3	±39.3	±23.7	±40.3	±13.7	±22.0	±29.2	±36.3	
Redhead (Aythya americana)	$\bar{x}$	0	0	0	0	0	0	0	0	40	0	0	802	0	0	60.1
	±S.E.	—	—	—	—	—	—	—	—	±95.5	—	—	±335.4	—	—	
Scaup spp. (Aythya spp.)	$\bar{x}$	0	0	0	0	4	2	0	0	45	69	38	53	0	0	15.0
	±S.E.	—	—	—	—	±3.1	±1.9	—	—	±21.6	±42.1	±25.5	±24.6	—	—	
Red-breasted merganser (Mergus serrator)	$\bar{x}$	10	0	1	2	0	1	0	0	0	0	1	1	15	12	3.1
	±S.E.	±10.1	—	±0.8	±1.9	—	±1.3	—	—	—	—	0.6	±0.8	±14.5	±6.1	
Surf scoter (Melanitta perspicillata)	$\bar{x}$	0	0	1	2	25	4	0	0	0	0	0	0	0	0	2.2
	±S.E.	—	—	±0.6	±12.9	±11.1	2.4	—	—	—	—	—	—	—	—	
Brant (Branta bernicla)	$\bar{x}$	0	22	0	0	0	0	0	0	0	3	0	0	0	0	1.8
	±S.E.	—	±23.3	—	—	—	—	—	—	—	±3.0	—	—	—	—	
American wigeon (Anas americana)	$\bar{x}$	0	0	0	0	0	0	0	0	0	0	6	16	0	0	1.6
	±S.E.	—	—	—	—	—	—	—	—	—	—	±5.7	±9.2	—	—	
Whistling swan (Cygnus columbianus)	$\bar{x}$	0	0	0	0	0	0	0	1	0	3.0	0	17	0	0	1.5
	±S.E.	—	—	—	—	—	—	—	±0.6	—	±1.8	—	±14.2	—	—	
Horned grebe (Podiceps auritus)	$\bar{x}$	8	0	2	0	1	0	0	1	0	0	0	0	1	0	0.9
	±S.E.	±4.2	—	±1.3	—	±0.6	—	—	±0.6	—	—	—	—	±0.7	—	
Canada goose (Branta canadensis)	$\bar{x}$	0	0	0	0	4	0	0	0	0	0	1	0	0	0	0.4
	±S.E.	—	—	—	—	±4.4	—	—	—	—	—	±0.6	—	—	—	
	(outside study area)	—	(966)	—	(438)	(333)	—	(1100)	(338)	—	(500)	—	—	—	—	
Pintail (Anas acuta)	$\bar{x}$	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0.3
	S.E.	—	—	—	—	—	—	—	—	—	—	±4.1	—	—	—	
Oldsquaw (Clangula hyemalis)	$\bar{x}$	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0.3
	S.E.	—	—	—	—	±2.0	—	±0.8	—	—	—	—	—	—	—	
Common goldeneye (Bucephala clangula)	$\bar{x}$	0	0	0	0	0	2	1	1	0	0	0	0	1	1	0.3
	±S.E.	—	—	—	—	—	±1.9	±0.7	±0.6	—	—	—	—	±0.5	±0.5	
Black duck (Anas rubripes)	$\bar{x}$	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0.1
	S.E.	—	—	—	—	—	—	—	—	—	—	—	—	±1.1	—	
Common loon (Gravia immer)	$\bar{x}$	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0.04
	S.E.	—	—	±0.6	—	—	—	—	—	—	—	—	—	—	—	

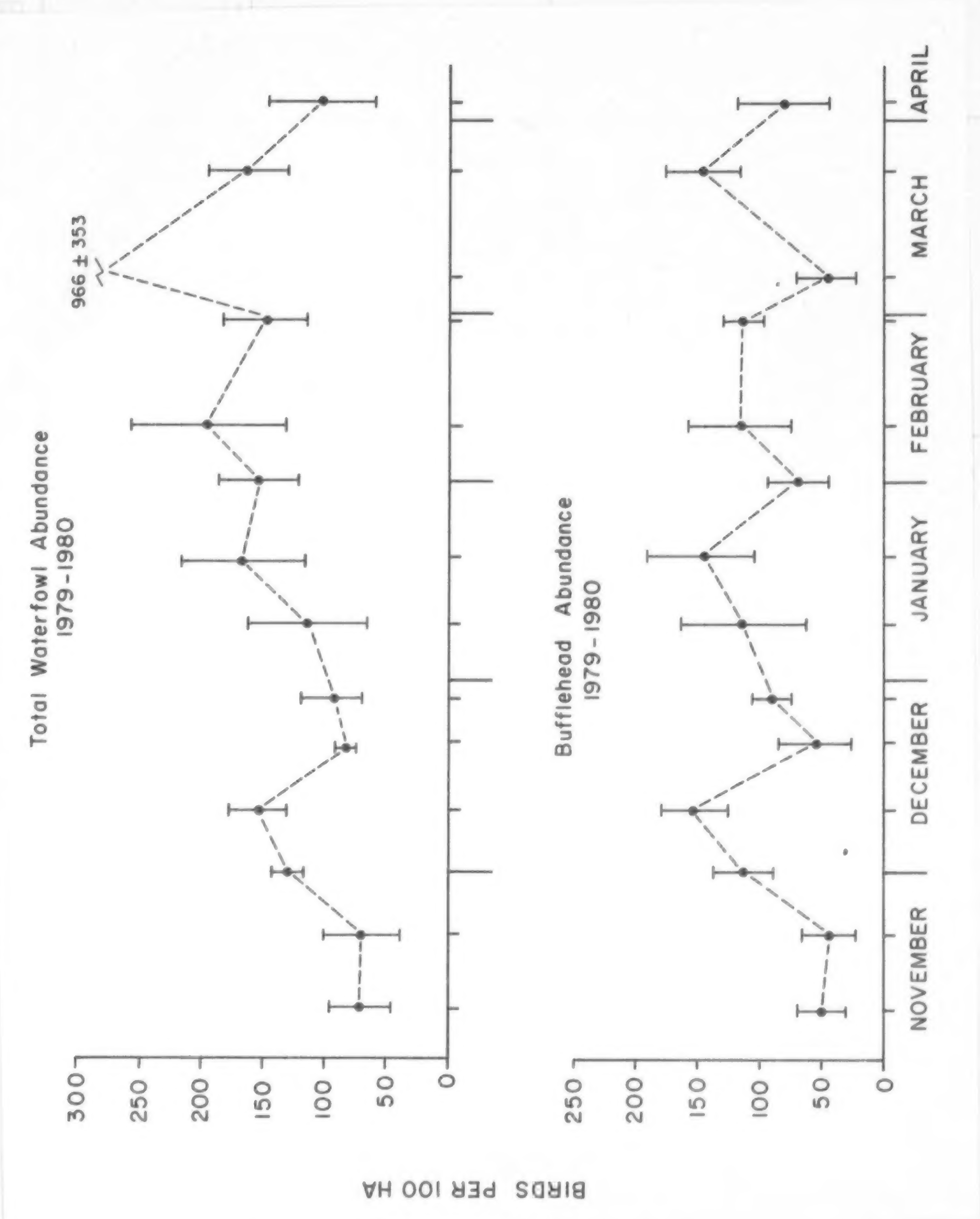

Fig. 5. Abundances of total waterfowl and buffleheads at Vaucluse Shores, area B-C 1979-1980. Points are means and bars are standard errors of the mean.

previous year, scaup (Aythya spp.) were important and were present in greatest numbers (45-60 per 100 ha) in February and early March.

In 1979-80 waterfowl abundance was independent of tide level, except in the shallow Ruppia zone, where numbers of birds were generally low but increased with higher tide levels (Figure 6). Rank correlation coefficients for the mixed and Zostera zones and the total study area were not significantly different from zero (Table 3).

Temperatures ranged from -6C to 22C but did not influence waterfowl abundance in the study area. Winds were predominately NNW, but direction had some effect on waterfowl numbers. A positive correlation was found between abundance and direction (from 10-360°), and higher numbers were associated with winds from the NNW ($p < 0.05$). Wind speed alone did not have a significant effect, but when wind direction was held constant, wind speed had a positive influence on bird numbers in the case of NNW winds ($p < 0.05$). When wind speed was held constant (in 5 knot increments) direction had a positive effect only at 21-25k ($p < 0.05$). No correlation was found between waterfowl abundance and time of day during daylight hours.

Within the grassbed, vegetation zone had a pronounced effect on waterfowl use (Figure 7). Mean densities of birds within these zones indicated an increasing inshore to offshore trend, with maximum densities in the Zostera zone. Numbers of birds were very low in bare sand and Ruppia, rarely exceeding one individual per hectare. Multiple comparisons indicated that these differences were highly significant for each pair considered (Table 4).

Again, few seasonal trends were evident in waterfowl abundance. A gradual increase in total numbers from January through March 1980 reflects primarily the occurrence of greater numbers of scaup and redheads, while bufflehead numbers fluctuated around the overall mean with no sustained increases or decreases.

Food Habits: Gizzard Analysis

Gizzards from 32 buffleheads were examined. Due to the difficulties of collecting waterfowl during active feeding, most gullets and a number of gizzards contained very little or no food. Of 25 esophagi collected, 22 were empty. Therefore, results are presented for gizzards only, two of which were completely empty and were also omitted from analysis. All other gizzards were analyzed regardless of fullness, in order to obtain an adequate sample size.

A total of 27 taxa were identified in bufflehead gizzards, including 23 invertebrate species, three plant species and fish vertebrae (Table 5). Molluscs and peracaridan crustaceans accounted for 18 of the 23 invertebrate species and the remainder included polychaetes, decapods, bryozoans and barnacles. Plant material in the

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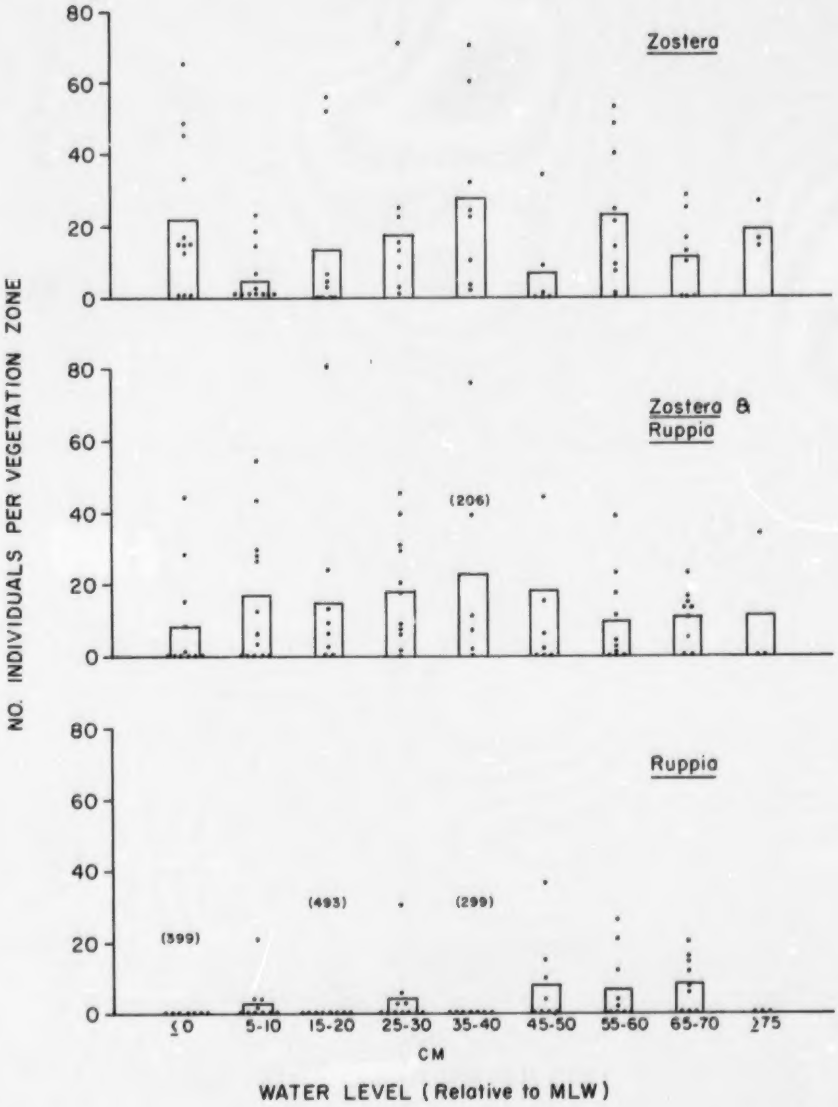

Fig. 6. Relationships between numbers of waterfowl and tide levels in three vegetation zones, 1979-1980. Numbers in parentheses refer to a single flock of redheads which were not included in analyses. Means are indicated by the height of blocks, and points are individual observations.

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TABLE 3. NONPARAMETRIC CORRELATION ANALYSIS OF WATERFOWL ABUNDANCE, 1979-1980.

					r_s
Tide Level	With	Abundance	Shallow	(*Ruppia*)	0.3128*
			Mixed		0.0881
			Deep	(*Zostera*)	0.0846
		Total Abundance			0.1002
Time of Day	With	Total Abundance			0.1463
Temperature	With	Total Abundance			0.0235
Wind Direction, Variable Speed	With	Total Abundance			0.2271*
1-5 knots	(N=9)				-0.3291
6-10	(25)				-0.2862
11-15	(20)				0.3807
16-20	(10)				0.1042
21-25	(5)				0.9487*
Wind Speed, Variable Direction					0.1837
NNE	(12)				-0.0808
ENE	(11)				0.0605
SSW	(5)				0.8208
WNW	(6)				0.6088
NNW	(35)				0.3281*

* $p<0.05$.

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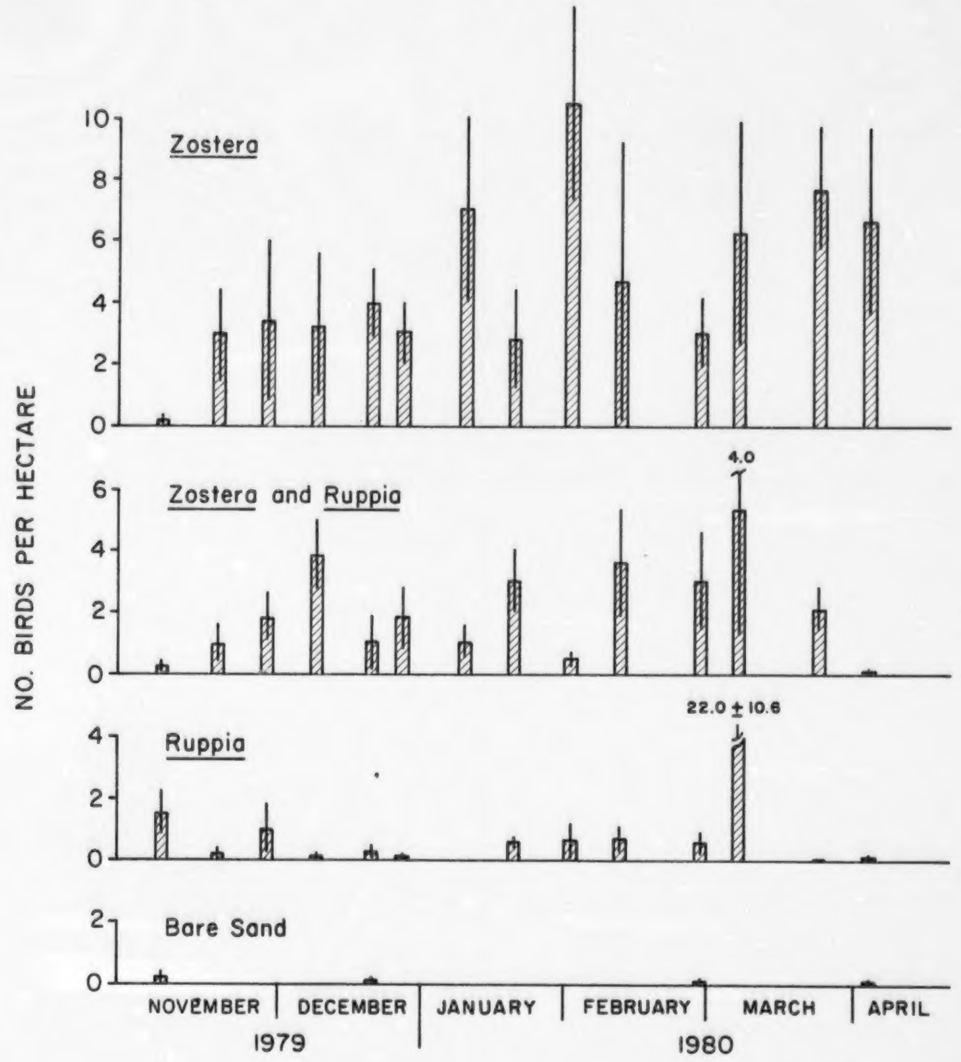

Fig. 7. Within-habitat variation in waterfowl density at Vaucluse Shores, 1979-1980. Means and standard errors are indicated.

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TABLE 4. EFFECT OF VEGETATION ZONE ON WATERFOWL DENSITY IN THE STUDY AREA. COMPARISONS TESTED BY THE WILCOXON STATISTIC U_s.

	Ruppia	Mixed	*Zostera*	U_s
Mean density (Birds/ha)	0.43	1.71	4.92	
± Std. Error	±0.110	±0.263	±0.697	
N=76				
Mean Ranks R/M	60.62	92.38	--	7021.0***
M/Z	--	66.30	86.70	5038.5**
Z/R	55.72	--	97.28	7393.5***

** $p < 0.01$
*** $p < 0.001$

TABLE 5. COMPOSITION OF GIZZARD CONTENTS OF 30 BUFFLEHEADS COLLECTED IN THE VICINITY OF VAUCLUSE SHORES, 1979-1980.

	Mean Abundance	Aggregate %	Mean Dry Weight (mg)	Aggregate %	Mean Ash-free Dry Weight (mg)	Aggregate %	Frequency of Occurrence %	IRI (DW)	IRI (AFDW)
Animal Contents									
Mollusca									
Gastropoda									
Crepidula convexa	49.4	32.8	43.0	24.6	4.3	16.4	76.7	22.0	18.9
Pyramidellidae sp.	20.2	16.3	12.9	9.6	1.3	6.1	66.7	8.6	7.5
Bittium varium	7.3	8.6	7.9	7.7	0.8	4.1	73.3	6.0	4.7
Astyris lunata	3.6	6.0	20.7	14.9	2.1	9.0	60.0	6.3	4.5
Acteocina canaliculata	0.7	1.6	1.3	1.5	0.1	0.8	30.0	0.5	0.4
Triphora nigrocinta	0.7	1.0	1.7	1.4	0.2	0.7	33.3	0.4	0.3
Nassarius vibex	0.2	0.6	9.8	5.5	1.0	4.0	16.7	0.5	0.4
Epitonium rupicola	0.1	0.3	0.3	0.2	tr	0.2	10.0	-	-
Acteon punctostriatus	tr	0.2	tr	0.1	tr	0.1	3.3	-	-
Bivalvia									
Anadara transversa	1.5	2.0	19.0	10.2	1.9	6.1	46.7	2.8	1.9
Gemma gemma	0.6	1.7	1.1	1.9	0.1	0.8	40.0	0.7	0.5
Annelida									
Polychaeta									
Nereis succinea	8.6	15.9	12.5	11.0	10.0	29.6	83.3	11.2	19.0
Arthropoda									
Crustacea									
Cirripedia									
Balanus improvisus	-	-	-	-	-	-	83.3	-	-
Malacostraca									
Crangon septemspinosa	0.2	0.2	8.7	4.5	6.4	5.0	6.7	0.4	0.2
Xanthidae sp.	tr	tr	0.2	tr	0.1	0.4	3.3	-	-
Mysidacea									
Neomysis americana	5.0	5.4	0.7	1.2	0.6	3.0	16.7	0.5	0.7
Isopoda									
Erichsonella attenuata	2.8	5.4	3.5	3.9	2.8	9.8	43.3	2.0	3.3
Edotea triloba	0.7	1.0	0.3	0.3	0.2	0.9	26.7	0.2	0.3
Idotea balthica	0.1	0.2	0.1	0.5	0.1	1.7	6.7	-	0.1
Paracerceis caudata	tr	tr	tr	tr	tr	0.2	3.3	-	-
Amphipoda									
Gammarus mucronatus	0.2	0.3	0.2	0.1	0.2	0.6	13.3	-	0.1
Cymadusa compta	0.1	0.3	0.1	0.1	0.1	0.4	6.7	-	-
Bryozoa spp.	-	-	-	-	-	-	60.0	-	-
Chordata									
Vertebrata									
Osteichthyes	-	-	-	-	-	-	36.7	-	-
Vegetation									
Zostera marina	-	-	-	-	-	-	70.0	-	-
Ruppia maritima	-	-	-	-	-	-	96.7	-	-
Zea mays	-	-	-	-	-	-	3.3	-	-

diet consisted primarily of Ruppia maritima and Zostera marina, with corn (Zea mays) present in a single gizzard.

Crepidula convexa was the dominant prey item by numerical abundance and dry weight, with a mean abundance of 49 individuals and mean dry weight of 43 mg per gizzard. In terms of ash-free dry weight, C. convexa was less important than the polychaete, Nereis succinea, which averaged 30% of gizzard contents by ash-free weight. However, abundance of N. succinea was relatively low (nine individuals per gizzard). Only chitinous jaws and setae of this polychaete were evident in gizzards due to rapid digestion of softer tissue, but numbers of individuals (and thus reconstructed weights) were obtained by counting pairs of jaws.

By taxonomic group, gastropods dominated gizzard contents (Figure 8). Of the five most important prey species by the index of relative importance (IRI) four were gastropods: Crepidula convexa, Pyramidellidae sp., Bittium varium and Astyris lunata. These four species accounted for nearly 60% of gut contents by dry weight (36% by AFDW) and 64% by abundance, and occurred with an average frequency of 70%.

Polychaetes were represented in gizzards only by Nereis succinea, although the contribution to the diet by this group may be underestimated. Bivalves (primarily Anadara transversa) and isopods (dominated by Erichsonella attenuata) were of roughly equal importance averaging from 5-12% of gizzard contents by dry and ash-free dry weight. Mysids (Neomysis americana) were abundant in several samples, but dry weight contribution was minor. Identifiable amphipods and decapods were encountered rarely and in low numbers.

The barnacle Balanus improvisus was a consistent prey species, with shell fragments found in 25 gizzards. Exoskeletal fragments of bryozoans were also found frequently (70% occurrence). Because numbers could not be determined for either of these groups, dietary importance was not assigned. Importance was not determined for plant material as no quantitative measure of percent composition was made. However, it appeared by visual estimate that vegetation was a minor dietary component, taken with invertebrate prey items found among vegetation.

Results of electivity calculations among mollusc prey species indicate that buffleheads may be at least partially selective (Table 6). Crepidula convexa was eaten in proportionally low numbers relative to its abundance in the grassbed, resulting in a significantly negative L value ($p < 0.001$) although it was still the dominant prey item. The gastropods Bittium varium, Pyramidellidae spp., Astyris lunata, and the bivalves Gemma gemma and Anadara transversa are apparently preferred (i.e. had significantly positive L values), but are found in much lower abundances in the environment than is C. convexa. The gastropods Triphora nigrocincta, Acteon

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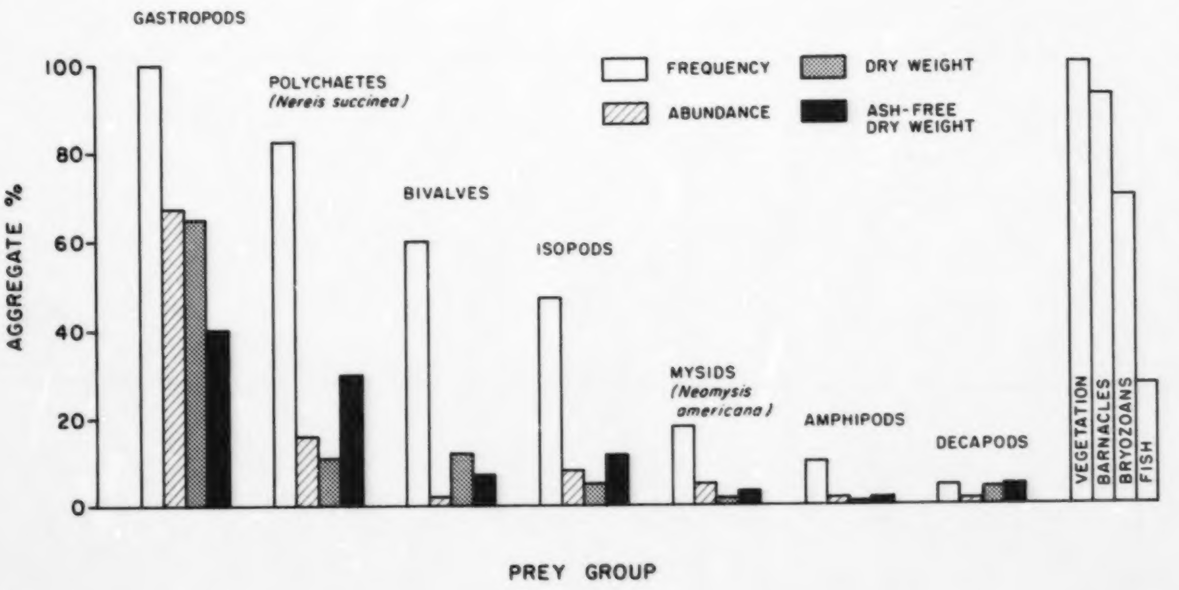

Fig. 8. Aggregate percent composition of gizzard contents, by major prey taxa, from 30 buffleheads collected in 1979-1980.

TABLE 6. BUFFLEHEAD DIETARY ELECTIVITY WITHIN MOLLUSCAN PREY SPECIES ONLY, AS MEASURED BY THE LOG OF JACOBS' ODDS RATIO (L) (GABRIEL, 1978).

Prey Item	% Abundance in environment	Mean % abundance in diet (n=15)	L	S.E. (L)	Z
Crepidula convexa	94.40	51.82	-2.75	0.270	-12.689***
Bittium varium	1.37	19.51	+2.86	0.290	9.872***
Pyramidellidae spp.	1.01	12.78	+2.66	0.343	7.770***
Anadara transversa	0.95	4.05	+1.49	0.583	2.563**
Gemma gemma	0.95	3.46	+1.35	0.580	2.326*
Astyris lunata	0.48	6.42	+2.65	0.473	5.613***
Triphora nigrocincta	0.46	0.64	+0.47	1.321	0.358 ns
Acteon punctostriatus	0.23	0.51	+0.79	2.213	0.359 ns
Acteocina canaliculata	0.15	0.58	+1.35	1.416	0.954 ns

* $p<0.05$
** $p<0.01$
*** $p<0.001$

punctostriatus and *Acteocina canaliculata* contributed to the diet in close proportion to their environmental abundances.

Food Habits: Stable Carbon Isotope Ratios

Bufflehead livers were fairly consistent in carbon isotope composition, with an average $\delta^{13}C$ of -17.2 ± 0.81 ^{o}/oo (Table 7). $\delta^{13}C$ values were obtained directly for 11 prey species (van Montfrans 1981) and were estimated by taxonomic group or feeding category for the remaining species (Table 8). In general, values were slightly less negative than bufflehead liver tissue and varied widely among taxa. The polychaete *Nereis succinea* (-13.3 ^{o}/oo), the gastropod *Bittium varium* (-13.4 ^{o}/oo) and the isopod *Erichsonella attenuata* (-13.4 ^{o}/oo) had the highest $\delta^{13}C$ values, while the gastropods *Crepidula convexa* (-20.2 ^{o}/oo), *Astyris lunata* (-16.4 ^{o}/oo) and the amphipod *Cymadusa compta* (-16.8 ^{o}/oo) were less $\delta^{13}C$-enriched. The suspension feeding bivalves *Anadara transversa* and *Gemma gemma* were assigned a value of -17.5 ^{o}/oo based on measured $^{13}C:^{12}C$ ratios for the clams *Mya arenaria* and *Mercenaria mercenaria*. Values for other prey species ranged from -14.0 to -15.9 ^{o}/oo.

From these values for prey items and the percent contribution of each species (by ash-free dry weight) to the diet, the resulting value for bufflehead tissue should approximate -15.4 ^{o}/oo, if all prey items are accounted for in correct porportions. Although this assumption was not strictly met, the observed mean was within 1.8 ^{o}/oo of the predicted value.

$\delta^{13}C$ values for other waterfowl species were also lower than most potential prey species (Table 9). With the exception of a single wigeon liver (-12.7 ^{o}/oo), values were even further removed from those obtained for submerged vegetation. *Ruppia* and *Zostera* ranged in $\delta^{13}C$ values from -7.5 to -10.6 ^{o}/oo, and the value for associated periphyton was -11.2 ^{o}/oo.

Waterfowl Exclosures

By 23 January, the inshore exclosures had been removed by ice, and results are presented for cages in pure *Zostera* only. Cage I in *Zostera* was sampled in January but not in March, as the top had been forced open for an unknown length of time. Instead, Cage II was sampled, and therefore the results from the two dates are not strictly comparable.

Samples from both cages (i.e. both sample dates) yielded significantly greater numbers of individuals and species than samples from uncaged areas (Table 10). Species abundances were significantly greater inside cages in approximately half of the comparisons ($p \leq 0.05$) (Figures 9 and 10). Eight species were found in significantly higher numbers in both sets of caged samples: the gastropods *Doridella obscura*, *Crepidula convexa*, *Astyris lunata*, and *Bittium varium*, a bivalve *Anadara transversa*, the isopods *Erichsonella attenuata* and

TABLE 7. CARBON ISOTOPE COMPOSITION OF BUFFLEHEADS COLLECTED NEAR VAUCLUSE SHORES, 1979-1980.

$\delta^{13}C$ Values Bufflehead Livers $^{o}/oo$	Date Collected
-15.8	12/18/79
-17.1	12/18/79
-16.4	12/18/79
-18.0	12/18/79
-17.2	12/18/79
-17.4	12/19/79
-18.0	12/19/79
-18.0	12/19/79
-17.8	12/19/79
-15.5	12/24/79
-16.8	12/26/79
-17.8	01/02/80
-17.0	01/14/80
-17.3	01/14/80
-16.5	01/15/80
-17.5	01/16/80
-18.4	01/16/80
-17.7	01/16/80
-17.6	01/16/80
-17.9	01/16/80
-16.4	01/23/80
-16.7	01/23/80
-17.0	01/23/80
-18.3	01/23/80
-15.3	01/23/80
-18.1	01/23/80
-15.3	01/23/80
-18.1	01/23/80
-18.5	01/23/80
-16.9	01/23/80
-18.0	02/22/80
-16.5	02/22/80
-17.3	02/22/80
-16.8	02/23/80

$\overline{X} = -17.2$ $^{o}/oo$
S.D. ± 0.81

TABLE 8. ISOTOPIC COMPOSITION OF BUFFLEHEAD INVERTEBRATE PREY SPECIES.

PREY SPECIES	$\delta^{13}C$ °/oo	PROPORTION OF DIET BY AFDW	CONTRIBUTION TO TOTAL $\delta^{13}C$
Crepidula convexa	-20.2	0.164	-3.31
Nereis succinea	-13.3	0.296	-3.94
Pyramidellidae sp.	-14.5[a]	0.060	-0.88
Bittium varium	-13.4	0.041	-0.55
Astyris lunata	-16.4	0.090	-1.48
Erichsonella attenuata	-13.4	0.098	-1.31
Anadara transversa	-17.5[b]	0.061	-1.07
Crangon septemspinosa	-14.2	0.050	-0.71
Neomysis americana	-17.5[b]	0.029	-0.51
Nassarius vibex	-14.2	0.040	-0.57
Triphora nigrocincta	-14.7[c]	0.007	-0.10
Edotea triloba	-15.5	0.009	-0.14
Gemma gemma	-17.5[b]	0.008	-0.14
Acteocina canaliculata	-14.7[c]	0.008	-0.12
Gammarus mucronatus	-15.9	0.006	-0.10
Idotea balthica	-14.0	0.017	-0.24
Cymadusa compta	-16.8	0.004	-0.07
Epitonium rupicola	-14.7[c]	0.002	-0.03
Acteon punctostriatus	-14.7[c]	0.001	-0.001
Xanthidae sp.	-14.5[a]	0.004	-0.06
Paracerceis caudata	-14.3[d]	0.002	-0.03

Total = Expected ^{13}C = -15.35 °/oo

[a] Mean value for: predator/omnivores
[b] " : suspension feeders
[c] " : gastropods
[d] " : isopods

TABLE 9. CARBON ISOTOPE COMPOSITION OF WATERFOWL OTHER THAN BUFFLEHEADS COLLECTED NEAR VAUCLUSE SHORES, 1979-1980.

Species	$\delta^{13}C$ Values $^{o}/oo$ (Livers)	Date Collected
Canada goose	-19.6	12/31/79
	-21.6	01/05/80
	-19.6	01/11/80
American wigeon	-19.1	12/17/80
	-17.6	12/17/79
	-16.2	12/17/79
	-16.8	01/01/80
	-15.0	03/14/80
	-16.2	03/14/80
	-12.7	03/14/80
Black duck	-18.8	01/01/80
	-17.8	01/02/80
Pintail	-16.9	01/11/80
Lesser scaup	-18.9	01/23/80
Greater scaup	-19.1	12/31/79
Oldsquaw	-16.5	01/16/80
	-17.7	01/23/80
Surf scoter	-17.1	01/01/80
	-18.3	01/01/80
Red-breasted merganser	-20.8	02/23/80

TABLE 10. NUMBER OF SEPCIES AND INDIVIDUALS FROM CORES TAKEN IN CAGED AND UNCAGED *ZOSTERA* IN JANUARY AND MARCH 1980. DIFFERENCES WERE TESTED BY THE WILCOXON STATISTIC U_s.

		No. Species		No. Individuals	
		Caged	Uncaged	Caged	Uncaged
January N=10		33	29	1257	854
		34	29	1615	937
		30	29	1264	1000
		31	29	978	1335
		32	29	1343	1027
		31	28	1002	941
		29	26	1360	930
		33	25	1153	694
		29	26	1089	620
		29	25	997	740
	$\bar{X}$	31.1	27.5	1025.8	907.8
	S	1.85	1.78	202.62	202.00
	U_s	92.5***		88.0**	
March N=10		45	41	1179	1161
		38	35	1504	1202
		34	32	1987	1522
		38	34	2154	1559
		39	31	2015	1741
		33	29	2013	1681
		41	29	2098	1444
		31	29	2316	1259
		43	33	2218	1079
		42	32	2607	1556
	$\bar{X}$	38.4	32.5	2069.1	1420.4
	S	4.58	3.66	297.55	230.16
	U_s	84.0**		95.0***	

** $p < 0.01$
*** $p < 0.001$

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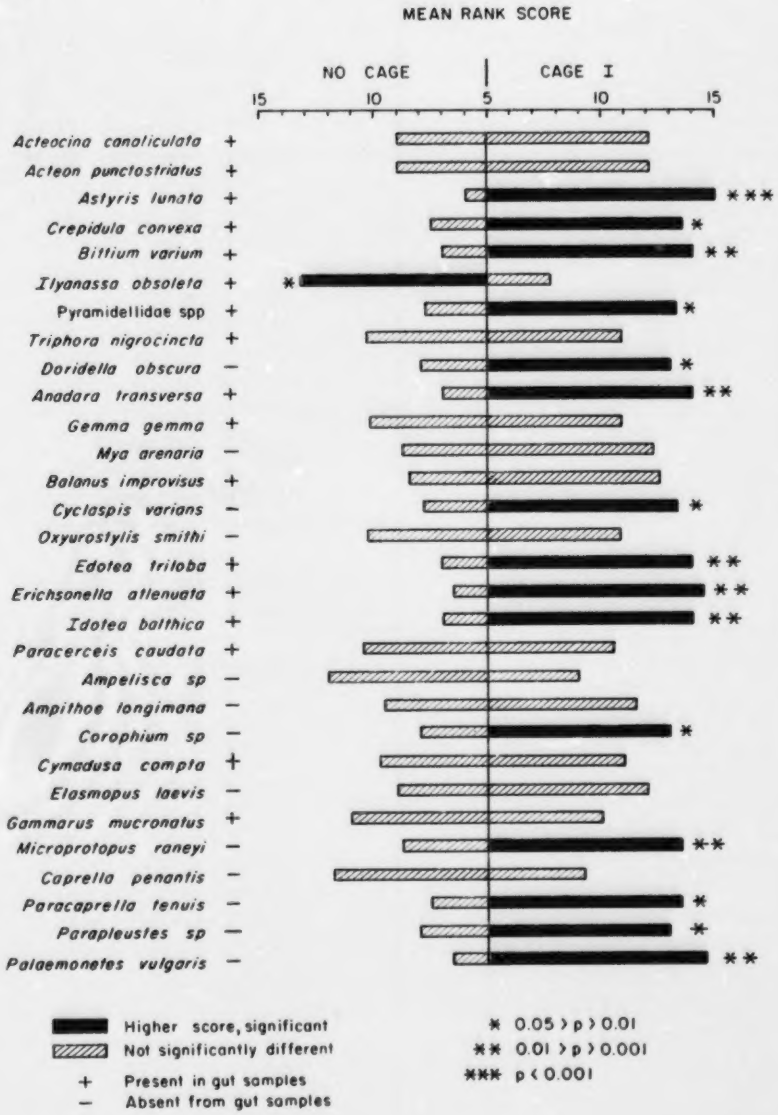

Fig. 9. Rank scores for species abundances in caged vs. uncaged samples taken in January 1980, as designated by the Wilcoxon 2-sample test. Expected score under H_o (that treatment means are equal) = 10.5. Significance level of the U statistic is indicated.

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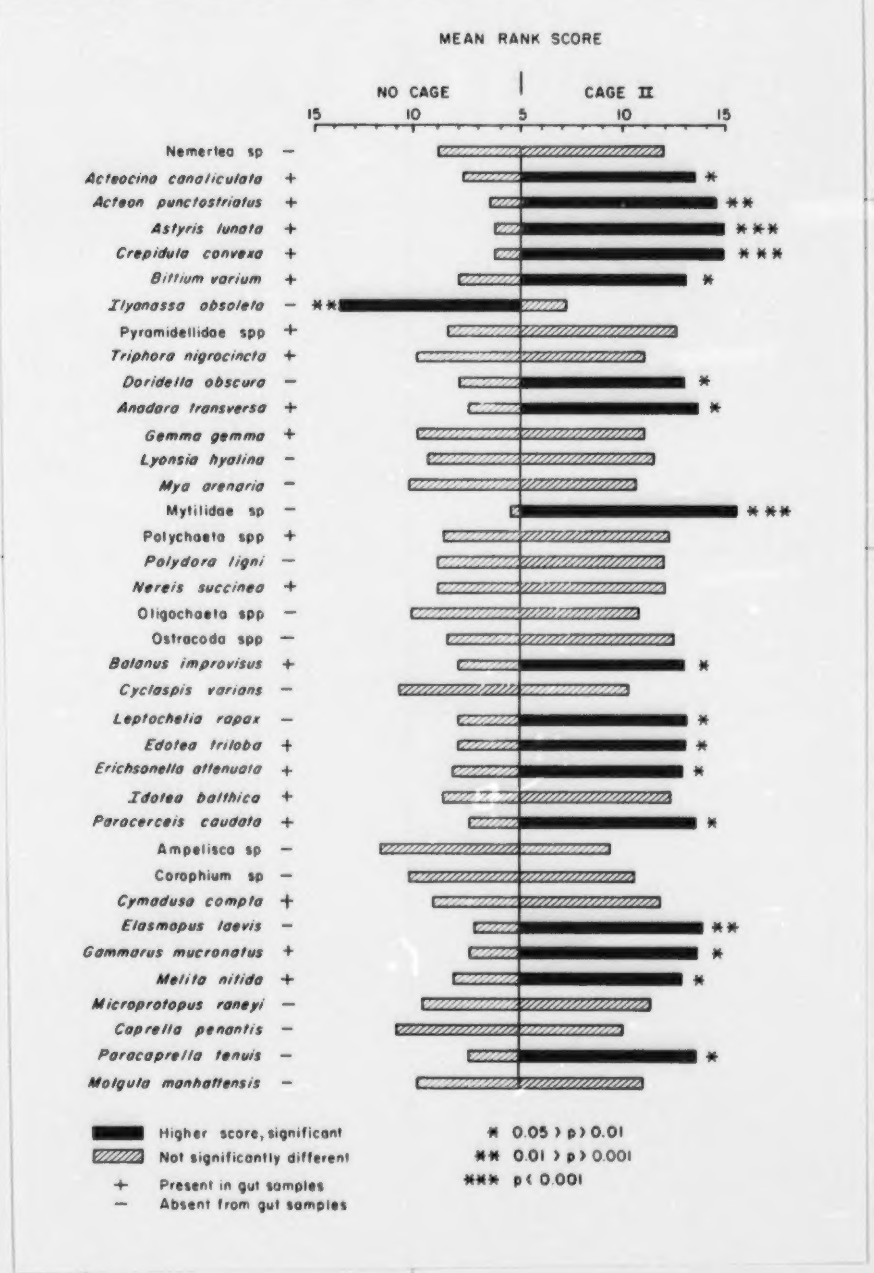

Fig. 10. Rank scores for species abundances in caged vs. uncaged samples taken in March 1980, as designated by the Wilcoxon 2-sample test. Expected score under H_0 (that treatment means are equal) = 10.5. Significance level of the U statistic is indicated.

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Edotea triloba, and an amphipod *Paracaprella tenuis*. With the exception of *P. tenuis* and *D. obscura*, all of these species were found in bufflehead gizzard samples, and most were important components of the diet. Other species with significantly higher abundances inside cages which were not present in gizzard or gullet samples included a number of peracarid crustaceans and juvenile blue mussels (*Mytilus edulis*). Only one species, the gastropod *Ilyanassa obsoleta*, was found in significantly higher numbers outside cages.

For most bufflehead prey species, the magnitude of the observed differences between treatments did not increase with the duration of the experiment, as indicated by a Wilcoxon test comparing these trends between January and March samples (Table 11). However, abundances of five prey species were significantly greater inside cages in March but not in January, and the reverse was true for two prey species.

Determinations of plant biomass indicated that the cage structure may have had a negative impact on plant survival and/or growth (Table 12). Orth et al. (1979) reported lower biomass values for *Zostera* in winter months, and a similar decline was observed from October to January in uncaged cores. However, biomass of vegetation inside cages was reduced to a greater degree, and the difference was significant ($p<0.001$) in March. Cages were observed to be badly fouled with macroalgae and hydrozoans at that time.

Differences in percent sand and silt-clay were not apparent between treatments in January or March (Table 13). Sediments were fine sands, with less than 15% silt-clay.

Consumption Rates

Total consumption estimated from waterfowl density in 1978-79 and 1979-80 amounted to 11.67 and 1.70 g AFDW m^{-2} respectively, over the entire area censused (Tables 14 and 15). In 1978-79 vegetation was the predominant waterfowl food, according to the general food preferences of abundant species. Foraging Canada geese removed approximately 8.26 g AFDW m^{-2}, or 74% of the total for vegetation. Brant, redheads, and whistling swans consumed 2.72 g, while the remaining grazers ate an estimated 0.18 g AFDW m^{-2}. If only the vegetated shallows are considered (approximately half the total area) the adjusted estimate for consumption of vegetation becomes 21.44 g m^{-2}. Of the total for animal material consumed by waterfowl in 1979, buffleheads and red-breasted mergansers consumed 92%, or 0.28 and 0.21 g AFDW m^{-2}, respectively.

In 1979-80, plant and animal foods were consumed in roughly equal proportions, although total consumption was an order of magnitude lower than in the previous year, reflecting primarily the absence of Canada geese. Redheads were the only important grazing species, removing 0.76 of the 0.88 g AFDW m^{-2} vegetation consumed over the entire area. Buffleheads and scaup were the only other abundant waterfowl, and together consumed 0.76 g of animal material per m^2.

TABLE 11. ABUNDANCES OF PREY SPECIES WHICH SHOWED SIGNIFICANT DIFFERENCES BETWEEN TREATMENTS IN JANUARY OR MARCH 1980 (INDICATED BY *). U_s COMPARES THE MAGNITUDE OF THESE DIFFERENCES OVER ALL SPECIES ACROSS SAMPLE DATES. VALUES ARE MEANS AND STANDARD ERRORS OF THE MEAN.

	JANUARY		MARCH	
	NO CAGE	CAGE	NO CAGE	CAGE
Crepidula convexa	22690 ±1937.7	28254* ±1643.7	12230 ±1171.6	21540*** ±1761.0
Pyranidellidae	280 ±81.0	825* ±254.1	328 ±88.3	468 n.s. ±88.4
Bittium varium	255 ±47.9	519** ±70.6	150 ±60.5	271* ±48.5
Astyris lunata	92 ±21.5	631*** ±166.7	51 ±20.3	541*** ±147.2
Erichsonella attenuata	370 ±31.9	796** ±174.1	382 ±71.7	573* ±87.8
Anadara transversa	169 ±33.9	306** ±30.5	80 ±15.2	188 ±36.6
Edotea triloba	427 ±99.3	936** ±113.7	946 ±83.9	1306* ±179.2
Acteocina canaliculata	57 ±27.6	121 n.s. ±51.5	22 ±13.5	121 ±34.5
Gammarus mucronatus	866 ±266.8	573 n.s. ±70.3	940 ±101.4	1436* ±175.6
Idotea balthica	373 ±30.0	675** ±82.6	248 ±46.9	338 n.s. ±53.3
Acteon punctostriatus	70 ±19.5	102 n.s. ±22.2	54 ±25.1	194** ±34.4
Balanus improvisus	99 ±28.3	213 n.s. ±52.2	48 ±13.6	140* ±36.8
Paracerceis caudata	204 ±19.1	201 n.s. ±35.2	89 ±20.6	201* ±44.3

$U_s = 88.0$ n.s.

TABLE 12. ABOVE AND BELOW-GROUND BIOMASS OF *ZOSTERA MARINA* FROM CORES TAKEN IN OCTOBER 1979 AND IN JANUARY AND MARCH 1980. DIFFERENCES WERE TESTED BY THE WILCOXON STATISTIC U_s.

	10/79		1/80				3/80			
			Uncaged		Caged		Uncaged		Caged	
	g m^{-2}		g m^{-2}				g m^{-2}			
	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below
	61.63	59.75	51.98	89.40	28.27	38.06	52.25	88.71	39.96	92.20
	76.40	114.86	45.72	114.17	46.11	46.18	38.66	77.78	23.73	134.84
	83.43	88.07	51.38	157.55	44.51	89.99	49.40	102.55	33.94	77.97
	81.70	66.87	57.25	74.75	54.02	118.87	39.75	89.44	39.26	134.44
	70.22	90.60	46.84	143.77	57.84	104.60	55.91	73.33	28.52	106.67
	61.73	198.24	57.11	59.39	22.84	91.25	45.12	94.09	38.34	79.66
			29.71	53.01	32.63	62.37	52.40	85.87	28.56	112.17
			54.32	100.29	33.14	128.65	48.90	58.31	23.08	88.36
			58.01	88.84	42.36	100.05	56.70	95.34	29.32	69.40
			68.55	119.04	58.69	144.50	62.20	63.05	32.26	50.90
$\overline{X}$	72.52	103.07	52.09	100.08	42.04	92.45	50.13	82.85	31.70	86.36
S	9.58	50.53	10.18	34.19	12.56	34.86	7.44	14.41	6.13	38.53
U statistic			72 n.s.	53 n.s.			97*** $p<0.001$	62 n.s.		

TABLE 13. COMPOSITION OF SEDIMENTS SAMPLED IN JANUARY AND MARCH 1980, FROM CAGED AND UNCAGED ZOSTERA. DIFFERENCES WERE TESTED BY A T-TEST, ON ARCSIN TRANSFORMED PERCENTAGES.

		% Sand		% Silt and Clay	
		Uncaged	Caged	Uncaged	Caged
January N=3		91.36	92.09	8.64	7.91
		91.64	92.68	8.35	7.32
		89.24	92.31	10.76	7.69
	$\overline{X}$	90.75	92.36	9.25	7.64
	S	1.315	0.297	2.329	0.638
	t	1.76 n.s.			
March N=5		93.68	89.81	6.32	10.19
		89.76	88.23	10.24	11.77
		88.83	86.04	11.17	13.96
		89.33	89.25	10.67	10.75
		92.45	90.03	7.55	9.97
	$\overline{X}$	90.81	88.67	9.19	11.32
	S	2.129	1.630	2.259	2.981
	t	2.00 n.s.			

TABLE 14. ESTIMATES OF CONSUMPTION BY WATERFOWL AT VAUCLUSE SHORES, 1978-1979, BY PREDOMINANT FOOD TYPE.

	Daily Consumption g AFDW ind^{-1}	Mean Abundance 100 ha^{-1} (total habitat)	Annual Consumption g AFDW m^{-2}
Canada goose	193.6	284.3*	8.26
Brant	120.6	46.1	0.83
Redhead	83.3	44.2	0.55
Whistling swan	308.1	29.9	1.34
American wigeon	62.1	12.0	0.11
Pintail	73.0	2.7	0.03
Black duck	85.8	2.2	0.03
Mallard	85.8	0.3	<0.01
	Vegetation (over total habitat)		11.15 g
	(over vegetated shallows)		21.44 g
Bufflehead	40.6	46.1	0.28
Red-breasted merganser	73.0	18.9	0.21
Common goldeneye	73.0	2.2	0.02
Scaup spp.	73.0	0.9	0.01
Surf scoter	75.6	0.4	<0.01
	Invertebrates/Fish (over total habitat)		0.52 g

* Foraging geese only.

TABLE 15. ESTIMATES OF CONSUMPTION BY WATERFOWL AT VAUCLUSE SHORES, 1979-1980, BY PREDOMINANT FOOD TYPE.

	Daily Consumption (g AFDW ind^{-1})	Mean Abundance 100 ha^{-1} (total habitat)	Annual Consumption (g AFDW m^{-2})
Redhead	83.3	60.1	0.76
Brant	120.6	1.8	0.03
American wigeon	62.1	1.6	0.01
Whistling swan	308.1	1.5	0.07
Canada goose	195.6	0.4	0.01
Pintail	73.0	0.3	<0.01
Black duck	85.8	0.1	<0.01
	Vegetation (over total habitat)		0.88 g
	(over vegetated habitat)		1.19 g
Bufflehead	40.6	96.1	0.59
Scaup	73.0	15.0	0.17
Red-breasted merganser	73.0	3.1	0.03
Surf scoter	75.6	2.2	0.03
Horned grebe	--	0.9	<0.01
Oldsquaw	59.3	0.3	<0.01
Common goldeneye	73.0	0.3	<0.01
Common loon	--	<0.1	<0.01
	Invertebrates/Fish (over total habitat)		0.82 g
	(over vegetated habitat)		1.09 g
	(over *Zostera* only)		3.32 g

Consumption by all other species totalled only 0.18 g AFDW m^{-2} over all habitat zones. Because the distribution of birds within these zones was recorded consumption of plant and animal foods was also calculated over the vegetated area (for all species) and the Zostera zone (for non-grazers). Utilization of the bare sand area was negligible and thus consumption rates are higher per m^2 of vegetation than when averaged over the entire habitat. Consumption of animal foods in the Zostera zone was approximately three times the rate averaged over all zones, reflecting higher bird densities associated with Zostera.

The results of the two methods used to estimate consumption of invertebrates in Zostera marina in 1980 are compared in Table 16. The disparity between measures was greatest in January, whereas in March the difference was negligible. Total consumption of six important prey species amounted to approximately 1.46 g and 1.43 g AFDW m^{-2} in January and March respectively by the exclosure method. Based on calculations from bird density, buffleheads, scaup and surf scoters removed 0.59 and 1.42 g of these prey species in January and March respectively, assuming a similar diet within this habitat for all three waterfowl species. Degree of agreement varied for individual prey speceis, and was generally poorer than between combined values.

Consumption estimates calculated for March are cumulative, and should approximate total annual consumption per unit area, for comparison with the fall standing crop of the same species (Table 16). Combined ash-free dry weight biomass was approximately 3.1 g in Zostera in October/November 1979 (data from van Montfrans 1981), or about twice the amount consumed by waterfowl.

DISCUSSION

Patterns of Waterfowl Abundance

Short term fluctuations in waterfowl abundance are difficult to interpret, and may relate to changes in conditions on the breeding or wintering grounds. Absence of Canada geese from the grassbed in the second year of this study, following high abundances in 1978-79, did not simply reflect local changes in wintering populations, as aerial surveys conducted by U.S. Fish and Wildlife Service and the Virginia Commission of Game and Inland Fisheries indicated similar abundances of this species in the Eastern Shore survey zone in both years (F. Settle, pers. comm.). Large flocks of geese rafting directly offshore from the study area in 1979-80 also indicated the presence of a comparable wintering population.

The intense foraging activity exhibited by Canada geese at Vaucluse Shores in 1978-79 is presumably atypical, as the species is primarily field feeding in the Chesapeake Bay (Stewart 1962, Munro and Perry 1981). Factors which influence such short term use of submerged vegetation are not clear, but possibly reflect the availability and accessibility of SAV in a given year. It is likely that when aquatic

TABLE 16. TWO ESTIMATES OF CONSUMPTION OF SIX IMPORTANT BUFFLEHEAD PREY SPECIES[a] IN *ZOSTERA*, COMPARED TO THE FALL STANDING CROP OF THESE SPECIES. VALUES ARE MEANS AND STANDARD DEVIATIONS.

	TO 19 JANUARY		TO 19 MARCH		
	1[b] gAFDW m^{-2}	2 gAFDW m^{-2}	1 gAFDW m^{-2}	2 gAFDW m^{-2}	Fall Standing Crop[c] gAFDW m^{-2}
Crepidula convexa	0.14 ± 0.111	0.48 ± 0.674	0.30 ± 0.590	0.81 ± 0.429	2.77 ± 0.859
Pyramidellidae	0.05 ± 0.041	0.04 ± 0.052	0.11 ± 0.220	n.s.	0.01 ± 0.013
Astyris lunata	0.08 ± 0.061	0.31 ± 0.314	0.17 ± 0.324	0.28 ± 0.264	0.03 ± 0.038
Bittium varium	0.04 ± 0.028	0.03 ± 0.032	0.08 ± 0.147	0.01 ± 0.309	0.01 ± 0.010
Anadara transversa	0.05 ± 0.041	0.18 ± 0.191	0.11 ± 0.219	0.14 ± 0.197	0.30 ± 0.311
Erichsonella attenuata	0.09 ± 0.066	0.42 ± 0.517	0.18 ± 0.351	0.19 ± 0.349	0.48 ± 0.275
Cons. by buffleheads	0.45 ± 0.348		0.95 ± 1.851		
By total waterfowl[d]	0.59 ± 0.795	1.46 ± 1.780	1.42 ± 3.617	1.43 ± 1.270	3.10 ± 1.506

[a] Polychaetes were not analyzed in January cage experiment, therefore *Nereis succinea* is not included.

[b] Estimate 1 = Bird Density x Daily Intake x Proportion in Diet x Days
Estimate 2 = Caged biomass - Uncaged biomass (n.s. indicates no significant difference between treatments).

[c] From abundance data (van Montfrans 1981).

[d] For estimate 1, refers to buffleheads, scaups, and scoters.

vegetation is abundant in a localized area, geese may switch from or supplement field feeding. Grain fields on the Eastern Shore of Virginia are often adjacent or very close to beds of submerged vegetation, and thus a temporary transition would not involve a redistribution of the population. This is especially important for Canada geese, as wintering flocks are highly organized socially, and members remain strongly attached to specific feeding and resting sites (Raveling 1979).

Goose foraging may have had a negative impact on SAV in the shallows in 1978-79, discouraging utilization the following year. However, several authors report comparable or more extensive depletion of SAV by waterfowl, yet do not infer a significant impact on vegetation (Kiørboe 1980, Jacobs et al. 1981). Alternatively, *Ruppia* may have been less abundant in 1980 for reasons unrelated to waterfowl grazing. Comparable biomass data are not available for both years, but researchers in the area noted a visible decline in cover of *Ruppia* in the shallows, and low abundance of this species was also reported in other areas of the Bay in 1980 (R. J. Orth, pers. comm.). The decrease in numbers and species of non-diving waterfowl as a group in 1979-80 may also reflect depleted SAV resources in the area, as non-divers are restricted to very shallow water for feeding and as a general rule, vegetation is the principle dietary component.

The importance of the bufflehead at Vaucluse Shores in both years of this study is consistent with the findings of Perry et al. (1981) that populations of this diving duck wintering in the Chesapeake Bay appear to be stable over the short term, and have shown a long term increase in proportion to increases in the flyway as a whole. Vegetation comprises a minor portion of the diet of buffleheads, and declines in SAV have not greatly affected its abundance or distribution (Perry et al. 1981). An invertebrate diet increases the range of suitable foraging habitats available to buffleheads, and this flexibility may partially account for the relative stability of wintering populations.

Species historically more dependent on submerged vegetation, such as brant and redheads, were infrequently observed at Vaucluse Shores but were occasionally very abundant. Brant are more typically found in coastal bays rather than estuaries, and now feed primarily on sea lettuce (*Ulva latuca*). Within the Chesapeake Bay, brant are abundant only where large areas of *Zostera* still exist (Stewart 1962). Redheads still rely on submerged vegetation, and therefore have declined in the Bay in response to declines in SAV. As with brant, they are concentrated only in areas with considerable coverage of SAV, such as Tangier Sound (Perry et al. 1981). Sporadic use of the study area exhibited by these two species thus reflects a currently patchy distribution throughout the Bay. Whistling swans and wigeon were relatively important in 1978-79 but the following year were nearly absent. Both species are primarily herbivorous, but whistling swans have recently begun field-feeding and include some animal material in the diet, whereas wigeon have not greatly altered food habits (Munro and Perry 1981).

In 1978-79 water depth was found to be important in determining the periodicity (via tide stage) of foraging by Canada geese. This relationship undoubtedly results from the behavior of up-ending rather than diving to obtain food, whereby foraging is restricted to very shallow water. Palmer (1976) states that timing of feeding in brant is governed by tide stage, food being more accessible at low tide. Jacobs et al. (1981) also found a relationship between low tide and numbers of waterfowl foraging in a *Zostera noltii* bed in the Dutch Wadden Sea. The area available to non-diving waterfowl for feeding is greatly increased at low tide, especially where the depth gradient is gradual, as is characteristic of seagrass meadows.

Tide level had little effect on foraging by waterfowl in the second season of study, as the most abundant species were diving ducks, notably buffleheads, redheads and scaup. Buffleheads will feed at all stages of the tide in areas where the preferred feeding depth of 2 to 3 m is not greatly exceeded at high tide (Erskine 1971). Redheads usually feed at depths less than 2 m, including extremely shallow water where they will feed as dabbling ducks if they cannot dive (Palmer 1976). Scaup forage at comparable depths, and are affected by tide level only when feeding grounds are completely exposed at low tide, in which case they cannot feed (Cronan 1957). In the present study the only significant effect of tide on waterfowl numbers in 1979-80 occurred in the inshore *Ruppia* zone, due to the fact that the area was often exposed at low tide or covered by only a few cm of water, which effectively excluded all waterfowl. The maximum depth in the study area at high tide was approximately 2 m, which is well within the preferred range of the above species.

The range of temperatures observed had no effect on waterfowl abundance, as ice formed rarely at the study site. Open water always remained in deeper areas and therefore birds could feed throughout freezing conditions. Time of day was not an important factor influencing numbers of birds present in the study area. Buffleheads moved in and out of the study area in small groups throughout the day, and did not exhibit obvious morning flights to the feeding area typical of many waterfowl species. Johnsgard (1975) notes that, while data are few, local movements of buffleheads on the wintering grounds are probably limited.

Waterfowl generally seek shelter from severe winds, which may account for the observed correlations between wind parameters and waterfowl numbers. At most stages of the tide, the sandbar which encloses the grassbed acts as a buffer to wave action, especially when winds fetch across or down the bay. Shoaling is more extensive at the extensive at the northern end and thus the sandbar offers more protection from NNW winds than from winds with a more westerly component. When winds are from the east or northeast, the entire western shore of the peninsula is equally protected and the study area offers no additional shelter. The presence of greater numbers of birds during strong NNW winds therefore reflects the orientation of the study area and the configuration of the protective sandbar.

Variation in bird density within the habitat in 1979-80 may be related to several factors. Densities were greatest in the *Zostera* zone, which approximates the preferred feeding depth of buffleheads (Erskine 1971) and is also the vegetated area farthest from shore. Avoidance of the inshore sand and *Ruppia* zones can be partially explained in similar terms in that these areas are very shallow and close to shore. Availability of food may be a more important factor. Abundances of epifaunal invertebrates were much lower in *Ruppia* than in the mixed and *Zostera* zones (van Montfrans 1981), possibly due to the shorter growth form and narrower blade width of *Ruppia*, and also its patchy distribution within the grassbed. The bare sand zone contained even lower numbers of invertebrates, with very few species of importance to foraging waterfowl. Nilsson (1969) also found that diving ducks in the Oresund fed over dense *Zostera marina* in preference to mixed areas with patchy cover, and that food resources were less abundant in the latter zones.

Bufflehead Food Habits

The importance of invertebrates in the diet of buffleheads is well documented, and small molluscs and crustaceans are the dominant prey in salt water habitats. Weimeyer (1967) found that buffleheads in the Humboldt Bay region fed primarily on bivalves, crustaceans, fish and gastropods and that the relative contribution of these groups varied between habitats. Erskine (1971) also emphasized the importance of crustaceans (mostly decapods and isopods) and molluscs as bufflehead foods on the wintering grounds. Nereid worms and bryozoans were cited as minor components of the diet. In these and other general accounts of bufflehead food habits (Cottam 1939, Stewart 1962, Munro and Perry 1981), diversity of food items is high, whereas Stott and Olson (1973) found that on the New Hampshire coast, sand shrimp (*Crangon septemspinosa*) comprised 75% of the diet of buffleheads.

Bufflehead gizzard contents analyzed in this study were dominated by species which are also abundant members of the epifaunal communities associated with *Ruppia* and *Zostera*, such as *Crepidula convexa* and *Nereis succinia*, suggesting that buffleheads rely heavily on commonly encountered animals. This agrees with the findings of Madsen (1954), who maintained that the diet of most diving duck species reflects the availability of prey. Stott and Olson (1973) also reported a close relationship between foods utilized by sea ducks and the abundance of these foods in preferred habitats. However, buffleheads in this study exhibited a degree of apparent electivity, with several species eaten in numbers disproportionate to their relative environmental abundances. Foraging behavior in buffleheads is probably similar to the closely related goldeneye (*Bucephala clangula*), which takes food items singly with a forceps action of the bill (Pehrsson 1976). Prey selection is enhanced by such a strategy and is limited only by bill morphology, visual acuity, and energy cost. A major difficulty in demonstrating electivity is that the relationship between numerical abundance and ecological availability is often unknown. Madsen (1954) stated further that among available (i.e. abundant) food items, the most easily obtainable within size limits are preferred. Thus positive selection may indicate real preference or degrees of availability, and for this reason the term apparent electivity is used.

Crepidula convexa was the only species which was apparently selected against by foraging buffleheads, although it was still the dominant prey item. This dark-shelled species lives attached to vegetation or hard substrates which, combined with the extremely small size of overwintering individuals (less than 2 mm average), may make it difficult to collect. Alternatively, some gastropods may move into the rhizome layer in the winter when above-ground vegetation is reduced (Marsh 1976), and may be encountered infrequently rather than avoided by diving ducks.

The gastropod *Bittium varium* is also dark in color, but is not firmly attached to vegetation and is conical in shape. It should therefore be more easily removed from blades by predators, although size in winter is comparable to *Crepidula convexa* individuals. The dove shell *Astyris lunata* and the bivalve *Anadara transversa* are larger (3-5 mm) and therefore more visible, which could explain the greater importance of these species in the diet relative to environmental abundances. Selection of pyramidellid gastropods is difficult to reconcile with the minute size of individuals (1.6 mm average) and the translucent nature of the shell. However, species of the genus *Odostomia* are reported to be ectoparasitic on other invertebrates, notably *B. varium* (Hyman 1967), and this association should increase availability.

Electivity studies inherently assume that the predator has fed in the same area where samples of prey abundance are taken. Because waterfowl are highly mobile, this may not always be true. In the present study, the presence of *Ruppia* and *Zostera* fragments in gizzard samples, as well as epifauna characteristic of the habitat, suggest that birds had fed either in the study area or in similar vegetated habitats.

Carbon isotope analysis also indicated the importance of SAV-associated invertebrates in the bufflehead diet. The difference between the mean $\delta^{13}C$ value for bufflehead liver tissue and that predicted from mean composition of gizzard contents and prey $\delta^{13}C$ values was within the 1-2 ^{o}/oo variation typically reported for such comparisons. However, the departure was in the negative direction whereas the shift is usually positive, resulting from metabolic processes which conserve ^{13}C (De Niro and Epstein 1978). It is likely that gizzard data used in this study to predict $\delta^{13}C$ values did not accurately reflect the diet, due to inadequate sample size or differential digestion of prey items. Gizzard analyses appear to have underestimated the nutritional contribution of species with more negative $\delta^{13}C$ values (primarily suspension feeders) rather than the softer-bodied polychaetes and crustaceans which had higher $\delta^{13}C$ values. Barnacles and bryozoans may account for most of the discrepancy, as these filter feeders were frequently eaten, but because only shell fragments remained in the gizzard, proportional contribution to total $\delta^{13}C$ could not be calculated.

Intraspecific variability in bufflehead $\delta^{13}C$ values (3.2 °/oo range) exceeded that suggested by Fry et al. (1978) for animals having the same diet (<1.6 °/oo). However, the low standard deviation obtained suggests that individuals did not vary widely in food habits, at least with respect to broad trophic groups. The greater variability in $\delta^{13}C$ values of food items and species composition of gizzard contents emphasizes the value of time-integrated data when describing food habits of species with highly mixed diets.

$\delta^{13}C$ analysis confirmed the minor role of submerged vegetation in the diet of buffleheads and most other waterfowl sampled. With few exceptions, waterfowl values were several parts per mil lower than those for Zostera and Ruppia, with considerable overlap between species having known preferences for vegetation (Canada geese, wigeon, pintails, black ducks) and the remaining species which rely more on animal foods. It is likely that terrestrial sources (especially agricultural grains such as corn and wheat) provide a large portion of vegetation eaten by Canada geese and possibly black ducks, as these plants are highly negative in $\delta^{13}C$ values (De Niro and Epstein 1978). Slightly more positive values exhibited by wigeon and pintails suggest a more substantial contribution by aquatic vegetation. Values for species with predominately animal diets were generally more negative than those for buffleheads, implying greater importance of suspension feeders or planktivorous fish.

Waterfowl Consumption Estimates

Submerged vegetation was an important resource for wintering waterfowl (primarily Canada geese) at Vaucluse Shores in 1978-79. If 80 g AFDW m^{-2} is considered a maximum early winter biomass value for Ruppia and stands of mixed Ruppia and Zostera, (R. J. Orth, unpubl. data) then waterfowl removed 25% of the standing crop in shallow water at the study site. A comparison of this estimate with those from other studies is attempted in Table 17, by standardizing all reported values to percentages of standing crop biomass, and restricting examples to studies conducted in the non-growing season. From these data, it is evident that the impact of waterfowl grazing varies widely among habitats and with waterfowl species composition and density. At Vaucluse Shores, grazing pressure was moderate in 1978-79 and minimal the following year, relative to previous estimates.

Apart from variable research conditions, a major difficulty with such comparisons is that consumption is often averaged over a large

TABLE 17. REPORTED OR CALCULATED ESTIMATES OF WATERFOWL GRAZING PRESSURE (% OF STANDING CROP CONSUMED) IN SAV HABITATS.

References	Habitat and Location	Estimated Grazing Pressure
Ranwell and Downing (1959)	*Zostera nana* *Zostera hornemanniana* Scolt Head Is., England	30-75%
Sincock (1962)	Submerged Aquatics Back Bay, VA and Currituck Sound, NC	20%
Steiglitz (1966)	*Halodule wrightii* *Ruppia maritima* Apalachee Bay, FL	32%
Cornelius (1977)	*Halodule beaudettei* Laguna Madre, TX	4%
Jupp and Spence (1977)	*Potamogeton* spp. Loch Leven, Scotland	13%
Verhoeven (1978)	*Ruppia cirrhosa* Texel, Netherlands	21%
Kiørboe (1980)	Submerged Aquatics Ringkøbing Fjord, Denmark	50%
Jacobs et al. (1981)	*Zostera noltii* Dutch Wadden Sea	50%
Wilkins (1982) (This study)	*Ruppia maritima* *Zostera marina* Chesapeake Bay, VA	25%

area, ignoring within-habitat variations in resource use. Jacobs et al. (1981) found that grazing pressure by geese and wigeon was not uniform in *Zostera noltii*, and was directly proportional to initial percent cover of vegetation. In the present study, bird densities, and therefore consumption rates, were much higher in the vegetated area than in the total habitat. Foraging by Canada geese was restricted to the shallows, further increasing consumption estimates in those areas. Variable consumption rates within a given habitat have also been reported for wading birds (Wolff et al. 1975) and diving ducks (Nilsson 1969), emphasizing the need to partition consumption within a habitat before attempting to estimate impact on benthic communities.

The results of exclosure experiments carried out in 1979-80 suggest that waterfowl had a significant effect on the abundances of a number of invertebrate species in the *Zostera* zone. By 19 March, when exclosures were removed, both estimates indicated a consumption of nearly 50% of the combined ash-free dry weight standing crop of six important bufflehead prey species. Qualitative agreement was obtained between the results of caging experiments and bufflehead gizzard analyses, in that species most affected were also important prey items. However, caging results obtained in January are diffcult to interpret on the basis of waterfowl foraging alone, with respect to these dominant prey species. Consumption calculated from exclosure samples was much higher than that based on bird density, and was within 0.03 g of the estimate for March. Waterfowl densities were comparable over the two intervals, and one would expect an increased difference between treatments in proportion to the number of days between sampling periods.

In studies where cages are used to exclude predators, the possibility of an artificial cage effect must always be considered. Larval settlement is enhanced by the current-baffling effect of the cage structure, and has been a major problem in previous caging experiments in soft-bottom habitats (Virnstein 1981). This effect was not demonstrated by sediment analyses in this study, although pipette analysis may not have detected slight changes in the silt and clay fractions. Increased sedimentation would have been expected from the degree of fouling that reduced the effective mesh size of the cages. In this habitat, however, few invertebrates which were significantly more abundant inside exclosures have free-swimming larval stages, and recruitment should not be affected by current velocity. *Crepidula convexa* exhibits direct development of larvae, with individuals hatched as juvenile snails (Ament 1979). The same is probably true for the gastropod *Astyris lunata*, and peracarid crustaceans are known brooders (Barnes 1980).

The prosobranch gastropod *Bittium varium* has a planktonic veliger larva, as does the bivalve *Anadara transversa*, but it is unclear whether reproduction continues into the fall. Marsh (1970) reported egg masses of *B. varium* in May and June in a *Zostera* bed in the lower York River, with juveniles predominant through the late summer and fall. Newly set individuals (0.5-0.7 mm) were not found in field collections at Vaucluse Shores in September 1979 (J. Lunz, pers. comm.) although bufflehead gizzard samples contained some individuals less than 1.0 mm. Information on the reproductive cycle of A. transversa was not available, but Marsh (1970) reported peak densities in August possibly indicating larval settlement. High densities of these two species may be related to the effect of the cage structure, but only if recruitment occurred after mid-October when exclosure experiments began. The high abundances of Mytilus juveniles in caged samples in March was almost certainly induced by the cage structure, as planktonic larvae are produced in early spring in the Chesapeake Bay, and Mytilus was not recorded in gizzard contents. The reverse trend for Ilyanassa obsoleta (higher numbers outside cages) may also be an artifact of the experiment, as I. obsoleta are attracted to artificial structures in order to deposit egg capsules and would therefore be found at the edges of the cages rather than in the sampled area (R. Orth pers. comm.).

The above comparisons between estimates of waterfowl consumption are made with caution, as confidence intervals on each estimate are very broad and many assumptions are involved in calculations. However, 1979-80 data suggest a range of values for annual consumption of invertebrates of approximately 2-3 g ash-free dry weight m^{-2} in Zostera marina, with lower values for the total habitat.

Few previous studies provide comparable estimates of the impact of waterfowl on invertebrates. Nilsson (1969) calculated that diving ducks consumed 9% of the total standing crop of invertebrates, or 22 g fresh weight m^{-2}, in the most heavily utilized part of the habitat. If this quantity is converted to ash-free dry weight and only the standing crop of prey species considered, the resulting values would probably be within the range obtained in this study.

Consumption by waterfowl at Vaucluse Shores was undoubtedly low relative to total standing crop biomass and annual production of invertebrates, but it was shown that significant cropping of dominant prey species occurred. Given the predominance of very small food items in the diet of buffleheads, this habitat represents an optimal feeding ground for the species, as the density and diversity of invertebrates are higher than in unvegetated areas. This research suggests that the interaction between waterfowl and the benthic fauna of SAV ecosystems is of greater trophic importance than has been previously recognized. Further long-term studies are required to more clearly define the role of non-grazing waterfowl in SAV habitats, and to determine and interpret patterns of direct utilization of submerged vegetation by grazing species.

SUMMARY

1. Canada geese were the dominant waterfowl at Vaucluse Shores in 1978-79, averaging 526 birds per 100 ha. Foraging by this species was influenced by tide level, with greatest activity around low

tide. An estimated 21.4 g AFDW m^{-2} of vegetation was removed by grazing waterfowl during the season, if bird density calculations are based on shallow vegetated areas. This represents approximately 25% of the estimated fall standing crop of vegetation.

2. The following year (1979-80), the waterfowl community in the study area was dominated by diving ducks, primarily buffleheads. Canada geese and other non-diving species were nearly absent, although local wintering populations were much the same size as in the previous year. Reasons for this marked contrast are unclear, but intense grazing in 1978-79 may have reduced the availability of vegetation in the shallows, or a decline in *Ruppia* biomass unrelated to waterfowl activity may have discouraged foraging in the study area in 1979-80.

3. In 1979-80, daily patterns of waterfowl abundance were influenced by wind parameters, whereas tide level, temperature, and time of day had little or no effect.

4. Differential waterfowl use of areas within the SAV habitat was found to occur in the 1979-80. Bird densities were greatest in the *Zostera* and mixed vegetation zones, and minimal in *Ruppia* and bare sand areas. The latter areas are very shallow and contain lower densities of invertebrates, and would therefore be less attractive to foraging buffleheads.

5. Bufflehead gizzard analyses indicated the importance of small gastropods such as *Crepidula convexa*, peracaridan crustaceans such as *Erichsonella attenuata* and the polychaete *Nereis succinea* in the diet of this diving duck. Predominant food items were also abundant members of the grassbed epifauna, although some evidence for selectivity was found. Carbon isotope analysis generally supported conclusions regarding bufflehead diet. Variability in bufflehead $\delta^{13}C$ values was low compared to the range obtained for food items, indicating a similar diet among individuals. These analyses confirmed the minor role of submerged vegetation as a direct food source for buffleheads and other waterfowl in the area in 1979-80.

6. Exclosure experiments yielded estimates of consumption of invertebrates which compared well with calculations based on bird density in March, and annual consumption in *Zostera* was estimated at 2-3 g AFDW m^{-2}. Approximately 50% of the fall standing crop of six important prey species was removed by foraging waterfowl in 1979-80.

7. These data suggest that waterfowl foraging may be an important, if unpredictable, component of energy flow in SAV habitats in winter months, both from direct consumption of vegetation and predation on associated epifaunal invertebrates.

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CHAPTER 7

TROPHIC RELATIONSHIPS IN A SUBMERGED MACROPHYTE BED BASED ON $\delta^{13}C$ VALUES

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ABSTRACT

Trophic relationships in a lower eastern shore Chesapeake Bay (Vaucluse Shores at the mouth of Hungars Creek) seagrass bed were investigated by examining time integrated stable carbon isotope ratios ($^{13}C/^{12}C$) in primary producer and consumer populations. The periphyton grazing snail, *Bittium varium* exhibited close ties to the microalgae found on *Zostera marina* leaves. Dominant isopods (*Erichsonella attenuata* and *Idotea baltica*) were more closely linked to the seagrasses themselves. In several other invertebrate and vertebrate species trophic relationships were more obscure although these will be more closely examined in a forthcoming publication. Overall, carbon isotope analysis appears promising as a method for elucidating general trophic relationships in seagrass communities.

INTRODUCTION

The natural proportions of two stable carbon isotopes, ^{13}C (1.1 $^{o}/o$) and ^{12}C (98.9 $^{o}/o$) are fractionated differentially by the various functional groups of primary producers depending in part on their photosynthetic pathway (Thayer et al., 1978). Vascular plants with the C_4 metabolic pathway tend to incorporate the ^{13}C isotope to a greater degree than those having a C_3 pathway (Hatch and Slack, 1970; Black, 1971; Welkie and Caldwell, 1970). For the purposes of comparing carbon isotope ratios in plant and animal tissues and those of inorganic substances, the δ (delta) ^{13}C index is used and is defined as:

$$\delta^{13}C(^{o}/oo) = \left(\frac{(^{13}C/^{12}C) \text{ in sample}}{(^{13}C/^{12}C) \text{ in standard (Chicago PDB)}} -1\right) \times 1000$$

Carbon isotope ratios fixed by plants remain relatively constant in both living and decomposing plant tissue (De Niro and Epstein, 1978; Haines and Montague, 1979). This ratio (i.e. $\delta^{13}C$ value) is maintained in a near one-to-one correspondence when transferred to herbivores specialized for feeding on a particular plant source and subsequently to higher trophic levels through carnivory or omnivory (Fry et al., 1978; De Niro and Epstein, 1978). Because $\delta^{13}C$ values can remain relatively unchanged throughout various trophic levels, consumer tissue $\delta^{13}C$ values reflect the organisms time-integrated dietary history. Thus, herbivores and their predators should reflect a narrow range of $\delta^{13}C$ values characteristic of the original plant substrate fed upon whereas species with a general feeding habit will have a broader range of values.

The primary producers which supply organic carbon for utilization by marine organisms such as those found in Chesapeake Bay grass beds include: seagrasses and fringing C_4 marsh plants such as Spartina alterniflora with $\delta^{13}C$ values from -9 to -13 $^{o}/oo$ (Thayer et al., 1978; Haines, 1976); benthic microalgae, mostly diatoms, with values from -16 to -18 $^{o}/oo$ (Haines, 1976); phytoplankton with ratios of -20 to -26 $^{o}/oo$ (McConnaughey and McRoy, 1979; Haines and Montague, 1979); C_3 photosynthetic plants showing values of -24 to -29 $^{o}/oo$ (Haines and Montague, 1979); and algae (no distinction between macro- and microalgae) with ratios ranging from -12 to -23 $^{o}/oo$ (Haines, 1976). Clues to the origin of those organic carbon sources should appear in tissue $\delta^{13}C$ values of the major grass bed utilizers and therefore shed light on the trophic structure of the grass bed community. The purpose of this section is to report on the preliminary results of trophic interactions based on $\delta^{13}C$ values found in primary producers as well as secondary resident and migratory consumers of the Vaucluse Shore grass bed. A more complete analysis and presentation of these data will be forthcoming.

METHODS AND MATERIALS

Tissue samples for $^{13}C/^{12}C$ carbon ratio ($\delta^{13}C$) analyses were collected throughout the summer of 1978 and 1979. Additional samples of waterfowl were collected during the winter of 1979-80. Plant material was carefully checked for epiphytes or epifauna which were removed by scraping or brushing prior to drying. Both the macrophyte and attached material were saved for analysis. Benthos and fish had their guts removed or were held in screened containers in aquaria for 24 hr to permit the voiding of gut contents. Specimens of resident consumers and predators were grouped by size. A special effort was made to examine changes in $\delta^{13}C$ values with growth. Shelled animals were treated with 10 $^{o}/o$ HCl prior to analysis to remove carbonate shell fragments. Waterfowl liver tissue was collected from freshly killed birds in the grass bed. All tissues collected were then dried, ground to a fine powder with a mortar and pestel or Wiley mill and distributed to consultants for further analyses. Some tissue samples were analyzed for $\delta^{13}C$ values by Dr. Evelyn Haines of the University of Georgia Institute of Ecology, Athens, Ga. The majority were analyzed by Drs. James Winters and Patrick Parker of Coastal Science Laboratories, Inc., Port Aransas, Texas.

RESULTS AND DISCUSSION

A wide variety of grass bed associated species representing different trophic levels and several feeding modes were analysed for $\delta^{13}C$ values (Table 1). The primary producers in the system had a wide range of values. Macroalgae exhibited $\delta^{13}C$ values between -16 and -19 $^{o}/oo$, epiphytic microalgae around -11.2 $^{o}/oo$ and submerged macrophytes had higher $\delta^{13}C$ values of between -7 and -10.6 $^{o}/oo$. Additional food sources sampled in the system which include or originate from primary producers are periphyton (i.e. microalgae and associated microfauna and detritus) found growing on the plants with $\delta^{13}C$ values of -18.3 and particulate detritus having $\delta^{13}C$ values of -16.3 $^{o}/oo$. Three sources of primary production with potential carbon input that were not sampled in this study but for which literature values exist include benthic algae, (mostly diatoms, with carbon isotope ratios between -16 and -18 $^{o}/oo$, Haines, 1976), phytoplankton (-20 to -26 $^{o}/oo$, McConnaughey and McRoy, 1979) and the fringing marsh vegetation consisting of Spartina alterniflora (-9 to -13 $^{o}/oo$, Haines, 1976). Some of these carbon sources can be detected in the invertebrates and vertebrates which inhabit or feed in the grass bed. For example a hydrozoan feeding on zooplankton had a value (-20.5 $^{o}/oo$) very near that reported for phytoplankton based food webs (-20 to -26 $^{o}/oo$, McConnaughey and McRoy, 1979). Similar plankton based food sources were indicated for other filter feeders such as adult epifaunal Crepidula convexa (-20.2 $^{o}/oo$) and Mya arenaria from the York River (-20.2 $^{o}/oo$) as well as red-breasted mergansers (-20.8 $^{o}/oo$) which consume primarily planktivorous fishes. Interestingly, several infaunal bivalve filter feeders showed somewhat higher than expected $\delta^{13}C$ values (-15.5 $^{o}/oo$) indicating perhaps the incorporation of some SAV detrital carbon.

The grazing gastropod, Bittium varium had $\delta^{13}C$ values (-13.4 $^{o}/oo$) approximating those of microepiphytes (-11.2 $^{o}/oo$) which confirm the utilization of eelgrass associated diatoms by B. varium. Species which show close trophic ties with SAV ($\delta^{13}C$ of -7.1 to -10.6 $^{o}/oo$) include the isopods

TABLE 1. MATERIAL COLLECTED FOR $\delta^{13}C$ ANALYSIS FROM THE VAUCLUSE SHORE STUDY SITE.

Species	Date Collected	Description and/or Feeding Type	$\delta^{13}C$
Plants and material of plant origin			
Algae	10/13/78	Primary producer	-17.7
Algae I	6/17/80	" "	-16.9
Algae II	6/17/80	" "	-18.7
Microalgae from *Zostera*	3/7/80	" "	-11.2
Periphyton on *Zostera*	6/17/80	Scum microflora(mostly diatoms) with associated microfauna and detritus	-18.3
Particulate grass bed detritus	6/17/80		-16.3
Zostera blade	3/7/80 6/17/80	Primary producer " "	-10.6 -7.1
Zostera roots	3/7/80	" "	-7.5
Ruppia blades	6/17/80	" "	-9.2
Ruppia roots	6/17/80	" "	-9.0
Hydrozoan	3/7/80	Zooplanktivore	-20.5
Polychaetes			
Glycera dibranchiata	6/17/80	detritivore (in Fauchald & Jumars, 1979)	-14.5
Nereis succinea	5/10/79 3/7/80	omnivorous (Bloom et al. 1972; Dauer, 1980)	-15.2 -13.3
Mollusks			
Crepidula convexa			
size range> 3.0 mm	3/7/80	filter feeder-adult (Hoagland 1979)	-20.2
size: 1.0-2.5 mm	6/17/80	grazer-juvenile	-17.2

TABLE 1 (continued)

Species	Date Collected	Description and/or Feeding Type	$\delta^{13}C$
Astyris lunata	3/7/80	Fam. Columbellidae-carnivore (Abbott 1974)	-16.4
Bittium varium	6/17/80	grazer detrivore algivore (this report)	-13.4
Ilyanassa obsoleta	5/10/79	deposit feeder (predominately)	-13.7
	3/7/80	but also scavenger (Barnes, 1980)	-14.2
from: Zostera	10/13/78		-14.0
Ruppia	10/13/78		-10.8
Macoma balthica	6/17/80	Deposit feeder (Reid and Reid 1969)	-15.1
Mya arenaria	6/17/80	filter feeder	
from: Vaucluse Shore			-16.1
York River			-20.2
Mercenaria mercenaria	6/17/80	filter feeder	-16.9
Isopods			
Erichsonella attenuata		omnivore or -herbivore?	
$\bar{x}$ length = 17.4 mm	5/10/79		-12.2
$\bar{x}$ length = 7.4 mm	5/10/79		-12.0
	3/7/80		-13.4
Length: 5.4-12.0 mm	6/17/80		-8.0
Length: 12.5-19.2 mm	6/17/80		-7.9
Idotea baltica		herbivore (Strong & Daborn 1979)	
	5/10/79		-11.0
	3/7/80		-14.0
Length: 1.7-6.5 mm	6/17/80		-8.7
Length: 5.3-12.0 mm	6/17/80		-8.9
Length: 9.4-23.9 mm	6/17/80		-8.9
Edotea triloba	3/7/80	omnivore or detritivore?	-15.5
Amphipods			
Gammarus mucronatus		algivore & detritivore (Zimmerman,	
$\bar{x}$ length = 8.9 mm	5/10/79	et al., 1979)	-12.5
$\bar{x}$ length = 2.2 mm	5/10/79		-12.8
length $\geq$ 3.0 mm	3/7/80		-15.5
length $\leq$ 3.0 mm	3/7/80		-16.3
	6/17/80		-12.4

TABLE 1 (continued)

Species	Date Collected	Description and/or Feeding Type	$\delta^{13}C$
Cymadusa compta	3/7/80	algivore & detritivore (Zimmerman, et al., 1979)	-16.8
Decapods			
Crangon septemspinosa	10/13/78	omnivore (Sanders et al 1962)	-14.1
	10/13/78	scavenger, predator,detritivore (Haefner 1979; Price, 1962)	-14.3
Palaemonetes vulgaris			
	10/13/78	predator (Nelson 1979)	-15.0
	10/13/78		-14.1
	10/13/78		-15.6
size class: <5.0 mm	6/17/80		-14.3
>5.0 mm	6/17/80		-13.5
Penaeus aztecas		omnivore-invertebrates, fish plant debris (Gosner 1971)	
tissue only	10/13/78		-13.3
muscle only	10/13/78		-13.3
Callinectes sapidus		predator/omnivore(Van Engel 1958)	
	10/13/78		-13.8
carapace width 5.0 mm	6/17/80		-12.7
carapace width 11-24 mm	6/17/80		-12.7
Fish			
Syngnathus fuscus	10/13/78	predator-zooplankton & motile crustaceans (Ryer in prep.)	-17.0
Bairdiella chrysura	10/13/78	predator-mysids & other paracarids (this report)	-15.22
Leiostomus zanthurus		omnivore-copepods, mysids, nematodes, plant material & detritus(this report)	
adult muscle tissue	10/13/78		-15.4
adult muscle tissue	10/13/78		-15.1
juvenile 37.8 - 23.1 mm total length	5/27/80		-13.1

TABLE 1 (continued)

Species	Date Collected	Description and/or Feeding Type	$\delta^{13}C$
Waterfowl			
Bufflehead	12/18/79	invertebrates,small mollusks, crustaceans,some submerged vegetation(Wilkins, this report)	-15.8
	12/18/79		-17.1
	12/18/79		-16.4
	12/18/79		-18.0
	12/19/79		-17.2
	12/19/79		-17.4
	12/19/79		-18.0
	12/19/79		-18.0
	12/24/79		-17.8
	12/26/79		-16.8
	12/26/79		-17.0
	1/2/80		-17.8
	1/14/80		-17.0
	1/14/80		-17.3
	1/15/80		-16.5
	1/16/80		-17.5
	1/16/80		-18.4
	1/16/80		-17.7
	1/16/80		-17.6
	1/16/80		-17.9
	1/16/80		-16.5
	1/16/80		-16.6
	1/23/80		-16.4
	1/23/80		-16.7
	1/23/80		-17.0
	1/23/80		-18.3
	1/23/80		-15.3
	1/23/80		-18.1
	1/23/80		-18.5
	1/23/80		-16.9
	2/22/80		-18.0
	2/22/80		-16.5
	2/22/80		-17.3
	2/23/80		-16.8
Oldsquaw	1/16/80	invertebrates,mollusks,crustaceans (Stott and Olson 1976)	-16.5
	1/23/80		-17.7

TABLE 1 (continued)

Species	Date Collected	Description and/or Feeding Type	$\delta^{13}C$
Lesser scaup	1/23/80	mollusks,submerged vegetation (Stewart 1962)	-18.9
Red breasted merganser	2/23/80	Fish(*Fundulus*,*Menidia*, *Alosa*) (Stott & Olson 1976)Crustaceans (Stewart 1962)	-20.8
Surf scoter	1/1/80	Bivalve mollusks (Stott and Olson 1976)	-17.1
	1/1/80		-18.3
American wigeon	12/17/79	primarily submerged vegetation (Stewart 1962)	-19.1
	12/17/79		-17.6
	12/17/79		-16.2
	1/1/80		-16.8
	3/14/80		-15.0
	3/14/80		-16.2
	3/14/80		-12.7
Pintail	1/11/80	emergent &submerged aquatic vegetation, some agricultural grain(Stewart 1962)	-16.9
Black duck	1/1/80	vegetation and invertebrates(Stewart1962)	-18.8
	1/2/80		-17.8
Greater scaup	12/31/79	mollusks, submerged vegetation(Stewart 1962)	-19.1
American coot	1/11/80	submerged vegetation(Stewart 1962)	-25.0
Canada goose	12/31/79	vegetation-agricultural grain	-19.6
	1/5/80	emergent & submerged aquatic vegetation(Stewart 1962)	-21.6
	1/11/80		-15.5

Erichsonella attenuata (-7.9 to -12.2 ^{o}/oo) and Idotea baltica (-8.7 to -14.0 ^{o}/oo).

Many of the remaining invertebrates showed intermedite ^{13}/C values ranging from between -11 to -17 ^{o}/oo. A complete interpretation of trophic relationships among these species must await a more detailed analysis of the data although at first glance these values imply considerable utilization of submerged macrophyte derived carbon.

Trophically important fishes in the grass bed included pipefish (Syngnathus fuscus), silver perch (Bairdiella chrysura) and spot (Leiostomus xanthurus) with δ^{13}C values from -13.1 to -17.0 ^{o}/oo. Other migratory consumers utilizing the grass bed included numerous species of waterfowl with a wide range of δ^{13}C values between species. Lowest δ^{13}C ratios were seen in the American coot (-25.0 ^{o}/oo), Canada goose (-21.6 ^{o}/oo in one individual) and red-breasted merganser (-20.8 ^{o}/oo). The low values observed for the former two species can possibly be explained by feeding on agricultural grains, primarily corn, which is readily available in nearby fields. The latter species, as already explained, feeds on planktivorous fish reflecting a plankton based food source. Buffleheads, for which a large number of liver samples were obtained, exhibited a fairly narrow range of values (-15.8 to -18.5 ^{o}/oo). These values closely correspond with those for the invertebrates which were important food items in bufflehead gizzards.

Although there was inadequate time to fully discuss the implications of our observed values, we expect to publish these results following a more complete evaluation and detailed comparison with other pertinent studies on this topic.

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